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THE MIGRATIONS OF ANIMALS FROM SEA TO LAND

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By

A. S. Pearse

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To

W. R. G. ATKINS

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A. S. P.

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ERRATA

Pearse's The Migration of Animals from Sea to Land

Page	13,	line	14:	for catalitic, read catalytic
"	30,	"	9:	for hardly, read hardy
"	44,	"	8:	for most, read more
"	45,	"	10:	for *Balamus*, read *Balanus*
"	50,	"	18:	for is, read are
"	61,	"	23:	after (Schlieper, insert 1929a;
"	73,	"	19:	for Ilionassa, read Ilyanassa
"	86,	"	28:	for hyptertonic, read hypotonic
"	96,	"	3:	for Oypode, read Ocypode
"	96,	"	20:	for oliochaetes, read oligochaetes
"	99,	"	9:	for siphunculids, read sipunculids
"	110,	"	7:	for annelids, read arthropods
"	118,	"	4:	for *litorea*, read *littorea*

CHAPTER I

INTRODUCTION

"We must interpret the present by the past" (Osborn, 1925).

"Science had to begin, not with problematical events from the past, but what actually happens before our own eyes" (Driesch, 1908).

PLANTS and animals cannot exist except in an environment. Those that dominate the earth today have struggled up a long evolutionary trail from the past. They perhaps began, when the earth was hot and even more or less molten, as inorganic substances in which carbon, nitrogen, oxygen, hydrogen, sulphur, iron, and other elements were combining to form such compounds as cyanide (Pflüger, 1875), water, carbon dioxide, ammonia, and acetylene. As the earth cooled, acetaldyhide, aldol, crotonic acid, and possibly even amino-acids formed (Kraft, 1931). At a certain stage in evolution when the environment had attained a stability which somewhat resembled the conditions that obtain today there came into existence protoplasmic, metabolic, self-sustaining, and self-perpetuating organisms. Once established, organisms began their evolution. As environments varied, many organisms became extinct. A few gradually progressed in complexity and ability and now dominate the earth. Today certain earth animals are able to sit in stable, automatically regulated environments that they have themselves made, and write treatises on the problems of science. Yet even proud man carries his heritage from the past. His blood plasma has

been called archaic sea water; during his embryological development piscine gill arches appear on the sides of his to-be neck; in adult life his bifocal vision and prehensile limbs remind him of ages long gone by when his ancestors lived in trees.

The characteristics of fossils indicate the nature of the environment in which the animals that formed them lived (Hubbard and Wilder, 1930). The great steps in evolutionary progress appear to have occurred when plants or animals surmounted the greatest environmental obstacles to invade new types of habitats where new earth resources could be utilized—when organisms left the ocean to take up life in freshwater and when they left the water for the land. This book is devoted chiefly to the consideration of such migrations.

Since early geological eras the composition of the ocean has changed. There was formerly less salt. At present sodium and magnesium are slowly increasing, but calcium and potassium are practically stationary. Calcium is continually added to and is continually precipitated out of sea water. The development of vegetation and soils on land has retarded the movement of potassium to the sea. "Briefly animal as well as vegetable protoplasm owes its relation to the elements sodium, potassium, calcium, and magnesium, to the composition of sea water which obtained when all forms were unicellular, just as the blood plasma owes its relations to the same four elements to the composition of sea water when prevailing circulating fluids were established. In other words, the relation of protoplasm to salts is due to the action of sea water, for incalculably long periods of time on the living matter of unicellular organisms" (Macallum, 1904). In particular areas at various times in the past there have been considerable changes in sea level. "Although the slow widespread rise and fall of the sea surface have produced important geological results, yet the existing raised beaches and the upward

growth of coral reefs into atolls are due to local variations in level of land, and not to general rise and fall of the sea" (Gregory, 1931).

ORIGIN OF LIFE

The origin of life remains a mystery. The only generalization based on evidence that biology has been able to make since the old, crude notions of spontaneous generation were disproved in the nineteenth century is "all life from life." Yet scientists have not been backward in proposing theories. Snyder (1909, 1911) believes that life was at first anaerobic and gives the following as his arguments: (1) many of the simplest organisms are today anaerobic; (2) fundamental cell processes are anaerobic, and oxidation is perhaps to be looked upon as only secondarily associated with life processes as a means of removing wastes; (3) aerobic life evolved from anerobic because of increased need for oxygen; (4) the need for oxygen increases with increase in body size; and (5) the oxygen in the atmosphere has come largely from the activities of plants and was not present in considerable amounts until plants had evolved to such a degree that they could manufacture it. Snyder also discusses the physical conditions which he believes were associated with the beginnings of life. He postulates such a sequence of activities as: (1) reactions of carbon dioxide and water vapor in a concentrated mixture under the influence of electrical discharges to produce formaldehyde or even formic acid; (2) the reaction of such compounds with ammonia or with amine or imine radicals, or with prussic acid to form simple amino acids; (3) the precipitation of colloidal substances in a solution containing metal salts, such as those of phosphoric acid, and resulting combinations; (4) coagulations, resolutions, and aggregations of particles; and (5) "the formation, through the chemical activity of these bioblasts, of an enclosing membrane, resulting in the first living

'cells'." Crile, Glasser, Telkes, and Rowland (1932) emphasize the formation and activities of nitrocarbons as a primary quality of life.

Donnan (1929) is convinced that the energy transformations of living cells conform with the first and second laws of thermodynamics, but believes that the mechanism for the harmonious coördination of organs and tissues is still a mystery. Pike (1929) grants that the first law of thermodynamics clearly applies to organisms but asserts that some doubt may exist about the second. However, he concludes that the second law does apply and that the entrance of sunlight into plants and its utilization as a source of energy are spontaneous processes. Life on the earth depends on radiant energy from the sun. The origin of life Pike believes to be associated with the appearance of certain carbon compounds which are capable of yielding energy at certain stages in stellar evolution. Oxidative processes are spontaneous and drive organisms on to increasing complexity. "The arrest of energy degredation in living nature is indeed a primary biological concept. Related to it, and of equal importance, is the concept of organization" (Hopkins, 1933).

Many thoughtful persons who have discussed the origin of life believe that organisms first came into existence in the sea. Rogers (1928) points out that living things must have originated when the temperature of the earth was between the freezing point of water and the coagulating point of proteins, when short wave lengths of light were more abundant than at present. He believes that colloidal particles in water were bombarded and that, associated with adsorption on colloidal interfaces, simple compounds of carbon, oxygen, hydrogen, and nitrogen were built up. In such a simple system phosphorus, sulphur, iron, and other elements were included. A catalyst of simple type helped the early colloid to become an energy transformer. Chlorophyll

is such a substance. Rogers believes that there was not one origin, but that living matter came into existence many times, probably always in the sea where there was appropriate temperature and when the sea water was more dilute than now. Allen (1923) also maintains that life arose in the sea and stresses the importance of photocatalysts acting on water, carbon dioxide, and simple compounds of nitrogen. Richardson (1928) pictures the origin of life in tropical intertidal pools along rocky seashores, and emphasizes colloids and pigments as factors.

Woodruff (Barrell *et al.*, 1926) has reviewed various theories of the origin of life.

THE SEA AS THE ORIGINAL HOME OF LIFE

In the oldest strata of sedimentary rocks which contain fossils the remains of plants and animals all appear to be marine. This indicates that life immediately before that time probably existed largely or wholly in the ocean. This of course does not preclude the possibility that life previously existed on land or in freshwater and became extinct without leaving records as fossils. However, "at the very beginning of the Paleozoic Era are found all of the main kinds of marine animals other than fishes" (Schuchert, in Barrell *et al.*, 1924). The invertebrates had been in existence during the preceding eras (Archezoic, Proterozoic) long enough for the chief types as they exist at present to become established. As time went on many of the older types (trilobites, etc.) became completely extinct and new types (chordates, etc.) came into existence. As evolution progressed certain forms that were related to early chordates (ostracoderms, arthrodires, etc.) and some that were clearly chordate (cyclostomes, elasmobranchs) appeared in the ocean, but bony fishes apparently had their origin in freshwater (Barrell, 1916; Noble, 1931).

The blood of all animals is saline. Many invertebrate animals that live in the sea have bloods which contain the same salts in the same proportions as those that are present in the surrounding medium. But the bloods of marine elasmobranch and bony fishes differ in salinity from sea water, the salt content being considerably lower. The bloods of freshwater and land animals also contain less salt than those of marine invertebrates (Pearse, 1932b). Sea water is a medium which contains all the elements which are necessary for building and maintaining protoplasm. The general similarity of the bloods of animals to sea water has been interpreted as indicating that all animals originated in the sea. To explain qualitative and quantitative differences which exist between the salts in the bloods of both marine and non-marine animals and sea water, some have assumed that blood salinities in certain cases became established and stabilized long ago when the salts in the ocean differed in amount from those which are characteristic today. Such questions will be discussed more fully in Chapter IV. While there are many discrepancies to be explained, it is a common belief that "blood is modified sea water" (Pantin, 1931).

The life histories and breeding habits of certain types of animals indicate that they originated in the ocean and subsequently migrated to land. For example, crabs and hermit crabs which live in the ocean generally pass through characteristic swimming larval stages; certain land crustaceans of the same types spend most of their lives on land but return to the ocean once each year and leave their young for a short sojourn in their ancestral home. The larvae which thus require a marine existence are quite like those of crabs which never leave the sea. On the Irish coast three species of the same genus of shore snails are arranged in zones. The snails of the species that is found at low tide lay eggs which hatch into swimming veliger larvae, and

these spend some time in the sea; those that live in the middle zone of the tidal area spend less time as swimmers; those that live near high-tide mark pass through their swimming stages before hatching from the egg and never swim. Such a series is believed to indicate origin in the ocean and varying degrees of adjustment to life on land (Colgan, 1910). Bony fishes appear to have originated in freshwater, and many of them breed there. Some fishes, like the salmon and shad, spend much of their adult life in the sea but spawn in freshwater, where their young live for a time. Such behavior perhaps indicates phylogeny from ontogeny but is refuted somewhat by the fact that certain fishes, such as the conger eel, live as adults in freshwater and spawn in the depths of the ocean. Some fishes of course live permanently in the ocean and breed there. Altogether considerable evidence from life histories and embryological development indicates that a number of types of animals originated in the ocean and gradually invaded freshwater and land habitats. The presence of gill arches in land vertebrates (reptiles, birds, mammals) during embryonic development means that such animals came more or less remotely from aquatic ancestors.

While it is generally admitted that life originated in the ocean there is much difference of opinion as to the exact region where it appeared first. There are some (Brooks, 1894) who believe that life first came into existence in the open sea, but most authorities (Simroth, 1891; Osborn, 1918; Johnstone, 1924) do not favor such a view, largely because there is a paucity of available nitrogen compounds there. Manifestly the lack of nitrogen, light, and other favorable conditions does not make it seem probable that life began in the depths of the ocean. Life is generally believed to have originated in the littoral region; perhaps in brackish water, perhaps even in freshwater or in wet soil.

Apparently no great groups (phyla) of animals originated except in the ocean (Hesse, 1920). The routes by which animals left the ocean and reached freshwater and land have been various. Some animals migrated directly across sea beaches; others ascended rivers, passed through marshes and swamps, or burrowed through soil. Some animals were transferred from the ocean by land elevations which isolated them in bodies of water which gradually became fresh. The ways animals followed from sea to land will be discussed in the next chapter.

Migration from the sea did not take place at any one time. It has occurred many times in the past and is slowly progressing on many shores today. Among all types of animals there is a continual tendency to spread into new available habitats in order to escape interspecific competition. The most successful animal colonizers of the land have been: (1) the arthropods, which have in many cases developed book-lungs or tracheae for breathing air; (2) the vertebrates, with lungs, dry skins, and toes; and (3) the snails, with slime and spirally coiled shells to prevent desiccation. Certain burrowing worms and many amphibians, which have little ability to conserve water within their bodies, are struggling to maintain themselves on land, and under favorable conditions some of these have even taken up life in trees. There are at present many examples of animals which are in the midst of their transformation from marine to freshwater, or from marine or freshwater, to land animals.

Not only have plants and animals migrated from sea to land, but there are countless instances where migrations have taken, and are taking, place in the opposite direction. Grasses, insects, reptiles, birds, and mammals have left the land for the sea (Lull, 1917; Pearse, 1932e). In general, primitive plants (Bews, 1923) and animals (Kennedy, 1928) have remained in primitive habitats, but after secondary migrations such relations may

become mixed. Migrations from water to land perhaps take place most readily in moist situations in the tropics (Harms, 1929).

Clark (1927) disagrees somewhat with current opinion concerning the origin of life in the ocean. He says: "The fauna of the sea is the aquatic fringe of the fauna of land waters, which were more extensive in the geologic past than now; the sea itself is practically sterile. Life is most abundant on the land where there is the maximum water vapor in the air as in the moist tropics; it is most varied where conditions are varied. . . . Life probably arose in marshy water (non- or slightly saline)."

The geological history of the earth and palaeontological history of plants and animals show that climatic changes have been rhythmical. Plants preceded animals on land (Case, 1919) and furnished basic food supplies. Land plants appear to have come from green algae (Bower, 1929), probably by direct migration from the ocean (Church, 1919, 1921, 1926). At first algae were probably pelagic, then sessile, and finally terrestrial. The reproductive organs of higher plants did not come from those of bryophytes but from algae (Church, 1926). Pollen permitted fertilization out of water (Bower, 1929; Campbell, 1930), and seeds furnished nutritious, concentrated food (Berry, 1920). At the beginnings and ends of epochs there were striking changes in climate which preceded marked readjustments and evolutionary changes in animals. Deformation of the earth's crust, volcanic dust, and variations in the amount of carbon dioxide in the atmosphere were important factors in producing climatic changes (Case, 1919). A monotonous environment may permit many individuals to exist but limits the number of types; whereas a changing environment is associated with variety and the evolution of new types (Clark, 1925). "Nothing is better established, amidst all the confusion of the discussions as to

method of evolution, than the fact that the environment changes before changes appear in organic forms" (Case, 1926).

COMPARISON OF OCEAN, FRESHWATER, AND LAND

"*Das Land ist das Reich der Gegensätze, das Wasser das Reich des Gleichmasses*" (Simroth, 1891). Water habitats in general are more or less stable; land habitats as a rule present extreme variability. An animal that lives in water is in no danger of death by loss of water from its body fluids, but may be easily killed by soluble poisons in the surrounding medium. Water is comparatively stable because it absorbs and loses heat slowly and cannot circulate rapidly. Shallow water may be subject to violent wave motions, and small stagnant bodies of water may be deficient in oxygen. Land animals have a dependable oxygen supply. The land is subject to wind storms, sudden and extreme changes in atmospheric temperature and moisture. As water is a dense medium compared to air, aquatic animals move slowly, while land animals may be speedy.

The ocean is in general more stable and uniform than bodies of freshwater because of its vast extent. Its high and varied salt content and relatively uniform temperature make it a favorable medium for protoplasmic activity. It is comparatively simple as an environment for plants and animals (Bigelow, 1931). It contains no nitrifying organisms except near shore. A wide variety of algae are present in the sea, but only about thirty species of spermatophytes occur (Buxton, 1926). All phyla of animals are represented in the ocean; echinoderms, brachiopods, and tunicates are found nowhere else. A considerable number of types of animals which had their origin in, or became adjusted to life in, freshwater or on land have entered the ocean. Bony fishes began in freshwater but now range through the ocean at all depths. Many extinct and modern reptiles took up life in the ocean. Whales, pinnipeds, and certain birds, like the albatross

and penguin, are truly oceanic, though their ancestors lived on land. Though insects are ubiquitous, aggressive, and dominant in many situations on land and occur in considerable numbers in freshwater, they have invaded the ocean very little. Alongshore are a few flies, midges, beetles, and apterous insects. Water striders run over the surface of the ocean in warm climates. Only one species of insect is submarine at all stages of its life cycle (Buxton, 1926; Tokunaga, 1930). However, if a pond is cut off from the ocean and becomes to some degree fresh, it is speedily invaded by insects—Diptera, Coleoptera, Odonata, Hemiptera, etc. (Pearse, 1932e). Cold sea water is more productive of life than that near the equator, perhaps because more trihydrol and oxygen are present in it. Trihydrol as colloidal water particles perhaps has a catalitic effect which favors the growth of aquatic organisms (Barnes, 1932a).

The freshwater areas of the world are isolated and limited in extent. Even the great lakes in Africa and North America are minute compared with the ocean. Freshwater is often variable in amount, as in swamps and rivers; is often subject to considerable variations in temperature, daily and seasonal, as in pools; and in various situations there may be wide differences in organic and inorganic content and reaction. In a shallow, stagnant pond or swamp where the surface is covered thickly with floating vegetation there may be no oxygen in the water at night. Such a condition is especially characteristic in the tropics. In eutrophic lakes the deeper waters may be without oxygen for months at a time. Notwithstanding the severity of the conditions of life in freshwater most of the phyla that began life in the ocean have also become established there, but there is usually less variety. Certain rather modern families (*Astacidae*, *Limnaeidae*, etc.), orders and even classes (Amphibia) are characteristic of freshwater, and do not often occur in the ocean.

Land plants and animals receive much energy directly from the sun and in the atmosphere have a dependable supply of oxygen, but they are frequently in danger of death by loss of water and must endure extreme fluctuations in temperature. Turbellarians, oligochaetes, polychaetes, onychophorans, myriapods, crustaceans, insects, arachnids, gastropods, and vertebrates are well established as land animals. Some of these are still obliged to live in moist situations, but such well-adapted types as certain snails, arachnids, insects, reptiles, birds, and mammals can exist even in deserts. Certain of the animals that have attained land life are of primitive marine stocks (Harms, 1929), but most successful land animals are modern, progressive types with impervious integuments and mechanisms for conserving water while breathing air.

In the four succeeding chapters the migrations of animals from sea to land will be considered in some detail: the routes the migrants followed; the reasons why animals left the dependable, stable ocean for a precarious life on land; the changes that have taken place in structures and functions of the animals that have succeeded in adjusting their systems of activities to land life; and the rewards that accrue to those animals that have struggled up the long difficult trails from the ocean and now view the world from mountain peaks. This has been the greatest emigration the world has known.

Chapter II

ROUTES FROM SEA TO LAND

PLANTS and animals that have left the ocean to dwell on land or in freshwater have been obliged to acquire new ranges of toleration to certain environmental factors. They have done this chiefly where environment permitted experimental trials without death. On ocean beaches, in estuaries, in marshes and swamps, in temporary pools, in isolated bodies of water in which salinity changes slowly, in soil where sudden changes in temperature are not possible and where desiccation is inhibited, and in a few other situations organisms are ever striving not only to continue to live but also if possible to spread into new types of habitats in which they have not lived before. Migrations from one realm to another commonly take place along the borderlines of territories, where there are more or less gradual or intermittent changes in environmental factors. No pelagic marine animal has ever transformed into a land animal.

BEACHES

On the beaches along the seashore the ebb and flow of the tides brings about a rhythmical change in water level, temperature, and other conditions of environment. Currents and waves transport and beat upon plants and animals and may bring about changes in salinity over a particular area. Plants and animals that live on ocean beaches, attached to the bare faces of rocks, safely ensconced in crevices or burrows, in rock pools, or even swimming in the littoral waters, live more or less both in

air and in water. Marine animals thus have opportunity to become adjusted to life on land, and land animals may gain some ability to endure life under water. Many thoughtful, beach-haunting biologists have suggested ocean shores as one route through which old marine stocks of animals have reached land (Flattely, 1920, 1921).

The moving littoral water contains myriads of small organisms which serve as food for animals. The accumulations which have been left along the drift line above high-tide mark furnish food and shelter for both terrestrial and aquatic animals. There is keen competition for places to live between tide marks. The plants and animals on beaches are arranged in zones. Various factors contribute to enforce such zonal arrangement: the height of tides, the slope of the beach, the character of the bottom, etc. On most beaches zones are clearly defined by characteristic littoral plants. These in turn furnish protection and food for animals. At one locality on Long Island, N. Y., for example, there are about five zones of plants: (1) the plankton (peridinians, diatoms, etc.) in the littoral water, (2) the attached bottom vegetation (Ulva, Enteromorpha, Fucus, Chondrus, etc.), (3) a mid-littoral belt (Spartina, Fucus, Ascophyllum, Bostrichia, etc.), (4) an upper littoral belt which has rather varied vegetation (Spartina, Scirpus, Salicornia, filamentous algae, etc.), and (5) supra-littoral belt containing a great variety of plants (Johnson and York, 1915). Similar zonal arrangement of animals is characteristic on all ocean beaches (Harms, 1929; Huntsman, 1918a; Pearse, 1914, 1914a, 1929, 1931; Verwey, 1930). It is apparent along the borders of coral reefs (Stephenson, Stephenson, Handy, and Spender, 1931) and also along those of freshwater lakes (Forel, 1892-1904; Muttkowski, 1918).

Migration from aquatic to land habitats takes place most readily when the atmosphere alongshore is humid (Harms,

1929; Lusk, 1917). The height which marine animals attain on beaches is more or less directly related to humidity (Fischer, 1927). On rocky shores marine crabs scamper in and out of the ocean most often at night, during rains, or when spray dashes high. In crevices animals can live higher than on exposed rock surfaces, because they are somewhat sheltered from wave action and desiccation. Along muddy beaches crabs and fishes wander into the adjacent land vegetation and often dodge into burrows. On clay and sand beaches most animals live in burrows and emerge only when humidity is favorable.

Air-breathing animals which take up residence between tides must migrate inshore at intervals or be able to endure submergence for several hours. Littoral mites can live for a couple of days under water (King, 1914). Intertidal insects have air stored in their tracheae, but also take advantage of small quantities of air which remain in crevices when the tide covers the beach.

On rocky coasts there are few or no plants at high-tide mark, but barnacles often occur in great numbers (Allee, 1923, 1923a; Pearse, 1914, 1929, 1931). Some rock barnacles are so situated that they are not covered by water except during the highest tides, which do not occur every day. A barnacle is typical of rock-beach animals—firmly attached; protected by a heavy calcareous covering against desiccation, extreme changes in temperature, and the pounding of waves; radial in symmetry and conical, so that waves easily slide over it; and adapted to catching food from water by spreading tiny, appendicular nets. A barnacle has long been used as an example of "retrogressive metamorphosis." During successive molts it changes from a free-swimming, appreciative (in that it has rather elaborate sense organs), and active animal to one that is unappreciative, sessile, and enduring rather than thoughtful. Such an animal as a bar-

nacle gives no promise of producing a land animal in the future. Its habits and inheritance make it psychologically unprogressive. The same is true of many other typical beach animals.

Sessile littoral animals have not become terrestrial (Harms, 1929; Pearse, 1922), yet there are a few of the active animals, such as certain crustaceans and snails, that apparently have progressed directly across sea beaches to land. At Tortugas the ability of a variety of littoral animals to live in the atmosphere and in various dilutions of sea water was tested. Most of the animals lived longer in the air than in the water. This suggests that they showed little tendency to migrate to land by first becoming adjusted to freshwater (Pearse, 1929). As has been stated, certain land crustaceans go directly to the ocean to breed each year. Cannon (1923) studied the development of the eggs of a land crab, *Cardisoma armatum* Herklots, in various solutions. He found that all eggs hatched in sea water; a few hatched in half fresh and half sea water; and all died in freshwater. Algae high up on beaches are more resistant to desiccation than those which live in lower zones and grow more slowly; snails at higher levels show greater negative geotropism and positive phototropism than those below (Colman, 1933). There are many evidences that animals have passed directly, but of course slowly, from ocean to land.

The little pools which are left between tide marks when the ocean periodically recedes serve as refuges for some marine animals and for some which are partially adjusted to life on land. The pools low down on a beach are less exposed to sun, wind, rain, trickling springs, and other aboceanic factors and maintain more constant temperatures than those which occur at higher levels. Animals which are characteristic of the former are on the whole more stenothermic than those in the latter (Klugh, 1921). Sometimes, after rains or along shores where springs seep out

over tide pools, a curious condition is established. A pool may be separated into a freshwater stratum above and a salty, marine stratum below. The pool may therefore be inhabited by certain aquatic insects, worms, and other freshwater animals which live above crabs, anemones, and other animals which belong to the ocean (Gersbacher and Denison, 1930; Pearse, 1914).

An ocean beach is a difficult place to live. There are low and high temperatures, strong tides, waves, desiccation, enemies which come inshore when the tide rises or run down from the land when the tide ebbs. Yet an abundant and varied fauna lives on ocean beaches. Advantages in the way of light, food, and oxygen apparently compensate for the disadvantages. Under the highly variable but favorable conditions on beaches some animals have undoubtedly become adapted to terrestrial existence.

ESTUARIES

Many types of animals have entered freshwater through estuaries. These have perhaps come in part from the "mud-line" which borders every continental shelf just beyond the limits of wave motion. "From the general character of freshwater species and from the almost complete absence of freeswimming larvae, we may suppose that the freshwater fauna has also been derived from mud-line animals which ascended from the mouths of great rivers and from estuaries" (Murray, 1895). Annandale (1922) maintains that a large proportion of the animals which leave the ocean to live in fresh and brackish water are primitive types which have been unable to compete with more progressive marine animals. He looks upon estuaries as "a refuge for spent races." In the Ganges Delta he found that most of the animals in fresh and brackish tidal waters were marine in their affinities, but few such animals were to be found in the river above. Annandale was impressed by the continual

pressure to enter new habitats which animals displayed, and surprised that so few marine species were able to establish themselves in the Ganges River. He affirmed that the attempts to invade freshwater were not anadromous or seasonal migrations but manifestations of a general tendency to spread. Pelseneer (1906) long ago expressed the view that river animals not only arose where temperatures were uniformly high, throughout the tropics, but also where the ocean was diluted by heavy rains. He cited Indo-China and the Bay of Bengal as a region which was particularly favorable for the transformation of marine into freshwater animals.

Any stream is subject to change in volume and level. The Amazon River may rise 12 to 50 feet during the rainy season. The Nile periodically overflows the bottom lands along its banks, and the Egyptians have long correlated their agricultural activities with its rise and fall. Some small streams are intermittent. Their beds are actually dry at certain seasons. The instability which is associated with variations in volume, speed, and level of stream waters is probably not of particular significance in relation to the migrations of marine animals into estuaries, for there is always a stratification of waters in the mouth of a river which empties into the sea. The fresh, usually warmer, water flows over the denser saline water from the ocean. Marine animals may therefore live in the deeper parts of a river without being in freshwater. There is also more or less conflict between tide and river current. When the tide flows, salt water may invade the mouth of a river, especially when a favorable wind drives the surface water upstream, but under ordinary conditions the surface of a river is fresh, even for some distance out into the ocean beyond the mouth. The yellow waters of certain of the great rivers which flow eastward along the coast of China give approaching vessels notice of their pres-

ence before land can be seen. The estuary of a river which flows into a sheltered bay or sound usually shows a graded series of salinities, often with extensive areas of brackish water which may remain relatively constant. Bourn (Weese, 1928) on the Atlantic coast of the United States studied salinities at 26 stations in a brackish-water area. He says: "There is no correlation between salinity and the rainfall. . . . Since there are no meterological tides in these inland waters, the salt content of Back Bay and Currituck Sound is governed by the force and direction of the winds. The influx of salt water in varying amounts has disturbed natural conditions and consequently, has greatly altered the aquatic life of the region."

Marine animals which burrow in some respects have a better chance to become adjusted to life in estuaries than those which live in the water above. "The water retained in the muddy foreshore of an estuary at low tide was more saline than the estuary water itself at the same distance from the sea. The retention of salt by the bottom and shore deposits may be a factor favoring the growth of burrowing animals in the central part of an estuary" (Alexander, Southgate, and Bassindale, 1932). But Fraser (1932) at the mouth of the Mersey River found the clam, *Mya arenaria*, only where sand and gravel were mixed with mud. "Mud of a very liquid nature apparently contains no fauna."

Suspended materials are constant factors which influence the lives of animals at the mouths of rivers. Estuarine animals often show special adaptations which enable them to live in water which is heavily charged with silt. Sessile animals must grow in length to rise above accumulating sedimentary deposits. Robson (925) states that the frontal width of an estuarine crab (Carcinas) decreases as water becomes more silty. Some estuarine species lack eyes; certain crustaceans are colored like their rel-

atives in the deep sea, which also live on soft, muddy bottoms. River waters generally contain more organic matter per unit of volume than the neighboring ocean (Johnstone, 1908). Some estuarine animals, such as oysters, depend for a considerable portion of their food on small organisms carried in flowing water.

About the mouths of many streams in the tropics there are extensive growths of mangroves. Such areas are particularly favorable for various animals, which find food, shelter, and suitable conditions for reproduction among the aerial roots and branches of these peculiar plants. Though the mud in mangrove marshes is usually soft and without oxygen, the plants furnish strata which are occupied by a variety of animals. Mangroves are not xerophytes, as are many plants which are found in salt or brackish water. They have a thicker epidermis in salt water; some species excrete salt through the leaves and are thus able to absorb salty water without raising the concentration in their tissues. In many ways mangroves are adapted for life on the soft muddy bottoms of estuaries.

Altogether, an estuary is usually a region where, though there may be wide variations in environmental factors, there are more or less extensive areas where marine, freshwater, or brackish-water animals may find favorable conditions for existence. At times curious associations of animals from various sources are found. Crayfishes and sunfishes may consort with swimming crabs; dolphins and king crabs live with river turtles and freshwater snails.

Working in two such widely separated estuaries as those of the Ganges and the Thames, Annandale (1922) and Robson (1925) are in general agreement concerning the origins and characteristics of estuarine animals. Annandale points out that the freshwater fauna of the world is quite cosmopolitan. The limnaeid and viviparid snails were already established in Creta-

ceous times. Animals of marine origin were present in the rivers of South America, Australia, China, India, and other regions. The Ganges River originated in the Tertiary Age. In its upper waters there are no marine animals in the "highly specialized fauna," but in the lower 900 miles there are four types which constitute the "relict fauna": (1) the dolphin, *Platanista gangetica* Lebeck, which does not leave the river, and is comparable to similar fluviatile dolphins in the Amazon and Yangtse rivers; (2) several species of the genus Navaculina, rather primitive clams belonging to the family *Solenidae;* (3) *Scaphula celox* W. H. Benson and *S. deltae* Blanford, clams; and *Ampelisca pusilla* Sars, an amphipod which also occurs in the Arctic Ocean. The euryhaline fauna of the Ganges Delta includes: sponges, a freshwater species and a boring sponge on shells; coelenterates, three widely distributed genera of hydroids and various species locally; polychaetes; an echiuroid; many snails and clams; several species of bryozoans; a king crab, *Carcinoscorpius rotundicauda* (Latreille), which has been seen in freshwater at Calcutta; various crustaceans, including amphipods, mysidaceans, shrimps, prawns, and crabs; fishes—anadromous, euryhaline, and estuarine; and a cetacean, *Orcacella brevirostris* Owen. There are few marine species in the river proper but many in the delta. "I cannot, however, find any definite dividing line between these two faunas. The relict fauna consists merely of organisms that have proved more capable of establishing themselves in abnormal circumstances and, therefore, more successful in the peculiar line of life adapted to them." Annandale believed that a slight change would enable other species to become established in the river above the delta. He cites a crab, *Varuna litterata* (Fabricius), as one species which migrates overland in vast numbers during the rainy season each year, but does not become established because crabs of the Family *Potamonidae* already occupy

favorable situations and can not be dislodged. A hydroid, *Campanulina ceylonesis* (Browne), also spreads continually but is eliminated in water which is so fresh that its specific gravity falls below 1.006.

As a result of his studies of the Thames River Robson (1925) states that there are usually three elements in an estuarine fauna: (1) permanent indigenous species, (2) seasonal migrants, and (3) stragglers. He found that a holothurian, a chaetognath, four molluscs, a few species of copepods, and a shrimp, *Palaemonetes varians* Leach, were restricted to brackish water. He agrees with Annandale that few marine species became established in freshwater by migrating through estuaries. Thorpe (1927) studied estuaries in Sussex, England, and reached similar conclusions.

Various species are doubtless kept from spreading from the ocean through estuaries into freshwater because salinity falls below their limits of toleration. In the estuaries of the Rivers Tamar and Lyner in Great Britain, Percival (1929) found that the number of marine species decreased greatly when salinity fell below 3%, but some persisted in salinity as low as 2.1%. Littoral species showed greater toleration for low salinities than others. In Holland, Redeke (1922) studied the distribution of brackish-water animals in relation to salinity and found that they were divisible into three groups as shown in Table I.

TABLE I

REDEKE'S (1922) GROUPS OF BRACKISH-WATER ANIMALS; HOLLAND

Oligohalinophil	Mesohalinophil	Polyhalinophil
Coccinodiscus rothi	*Coccinodiscus biconicus*	*Coccinodiscus grani*
Thalassiosira baltica batava	*Thalassiosira baltica*	*Thalassiosira excentrica*
Chaetoceras mülleri	*Chaetoceras subtile*	*Chaetoceras debile*
Eurytemora affinis	*Eurytemora hirudinoides*	*Eurytemora hirudo*
Gammarus pulex	*Acartia bifolosa*	*Acartia discaudata*
	Gammarus locusta	*Gammarus locusta*
	Corophium lacustre	*Corophium lacustre*
	Corophium grossipes	

At the mouth of the Elbe River, Schienz (1923) studied the distribution of 21 species of crustaceans between Hamburg and Cruxhaven, where salinities ranged from 0.47 to 17.12. His list included 1 crab, 1 shrimp, 3 schizopods, 10 amphipods, and 6 isopods. All these except one isopod (Asellus, which was only found in freshwater), occurred at the mouth of the river and gradually disappeared upstream. Only one species, *Gammarus locusta campylops* G. O. Sars, ranged throughout the region. Schienz numbered his stations from the mouth upstream, 1 to 26. The ranges of the species were as follows:

Species	*Stations*	*Lowest Salinity*
Crago vulgaris (Fabricius)	1–13	0.43
Carcinas maenas Fabricius	1–8	6.82
Neomysis vulgaris Thompson	1–23	0.37
Praunus flexuosus Müller	1–5	13.50
Macropsis slabberi (V. Beneden)	1–4	13.97
Corophium curvispinum devium G. O. Sars, Wundsch.	20–26	0.0–0.5
Gammarus locusta campylops G. O. Sars	1–26	0.37
Corophium lacustre Vanh.	8–14	0.37
Gammarus duebenii Liljeborg	1–10	4.40
Corophium volvulator (Pallas)	1–9	5.90
Leptocheurus hirsutimanus Zadd.	9	5.90
Orchestia gamarellus (Pallas)	1–4,9	5.90
Gammarus locusta (L.)	1–6	13.15
Gammarus marinus Leach	1–5	13.50
Taliturus saltator (Mont.)	1,5	13.50
Asellus aquaticus (L.)	17,21–26	0–0.5
Sphaeroma rugicauda Leach	5–9	5.90
Idothea viridis G. O. Sars	1–6	13.15
Jaera marina (Fabricius)	1–4	13.97
Idothea baltica (Pallas)	1–3	15.36
Ligyda oceania (L.)	1–3	15.36

Clearly these crustaceans fall into three groups in their relations to salinity.

Prenant (1929) has called attention to the fact that the distribution of marine species in estuaries is correlated with respiratory requirements. As water becomes less saline, respiration

becomes more difficult. The circulation of water by currents may in part compensate for the difficulties associated with lowered salinity. Of course variations in salinity have other effects on organisms besides those connected with respiration. These will be considered more fully in Chapter III (pp. 59-67).

There are a few animals which can survive direct transfer from ocean to freshwater, and there are many marine animals which live at times in freshwater or in diluted sea water (Pearse, 1929; Schlieper, 1929a; Sumner, 1906; Vaughn, 1919). As would be expected, small marine animals usually have less ability to live in diluted sea water than large animals. Young animals are generally less resistant but often possess "greater capacity to acclimate" (Andrews, 1925). Invertebrates with hard exoskeletons or slimy coverings are more resistant to changes in salinity than those without such protection. Brues (1927) kept a portunid crab, *Callinectes ornatus* Ordway, alive in freshwater for three months. Along the coast of Holland shrimps (*Crago vulgaris* Fabricius) migrate from salt to brackish water in spring, and immature individuals move further inland than adults (Havinga, 1930). According to Harms (1929), 22 species of selachians are established in freshwater, and tides have been an important factor in facilitating their passage through estuaries. The clams belonging to the Family *Dreisensidae* have apparently spread from the Black Sea and established typical species after entering rivers (Andrusov, 1897). The Black Sea was probably more salty and characteristically marine in the past than it is now.

In estuaries all types of spreading animals are not moving upstream. Some freshwater species are making progress toward the ocean. For example, various lines of evidence indicate that insects had their origin on land. Many of them have since invaded freshwater and a few have become established in or on

the sea. Several species of water striders skim over the surface of the open ocean. The more specialized insects appear to be able to endure high salinity better than more primitive types (Buxton, 1926; Thorpe, 1927). Chironomid larvae endure variations in salinity better than corixids. Among the insects as a whole, the flies (Diptera) have been the most successful colonizers of the sea. Some of them live in water which is much saltier than the ocean (Beattie, 1932; Pearse, 1931, 1932e; Vogel, 1927). Bony fishes appear to have originated in freshwater and to have spread to all parts of the ocean.

An estuary has been called "the doorway by which marine forms have populated freshwater." This statement is perhaps true, but an estuarine doorway is not wide open and easily passed. There are many difficulties to be surmounted. Many animals struggle long ages to get through and fail. Only a few attain freshwater by this route.

POOLS, SWAMPS, AND MARSHES

Marshes and swamps resemble estuaries and are often connected with them. They are always shallow; the amount of water in them varies more or less at different seasons; they contain considerable submerged and emergent vegetation, such as eel grasses, potamogetons, rushes, and grasses. A salty or brackish marsh near the sea may be subject to tidal influences; a freshwater inland swamp may be overflowed during heavy rains or become nearly dry at other times. Pools are like marshes and swamps in many respects, but are largely without emergent aquatic vegetation.

Stagnant, shallow, vegetation-filled bodies of water near the ocean often tend to become fresher. In a Long Island, N. Y., salt marsh Conrad and Galligar (1929) found that freshwater vegetation advanced seaward and that saltwater plants retreated

before them. Such migrations were in part due to the filling in of the land. On the coast of Tunis in areas which are periodically submerged by the ocean, dried, and subjected to rainfall, only ephemeral halophytes grow; but in similar areas which are not submerged, marshes develop in which Salicornia is the dominant plant (Burollet, 1926). Salt in itself is apparently not the chief factor in making the difference between an ocean beach and a marsh, but several factors are concerned. Animals which live in marshes, swamps, and pools are often subjected to extreme variations in temperature, salinity, essential gases in the water, and in available water. In a South American tropical swamp Carter and Beadle (1930) found that fishes survived temperatures as high as 42°C. during the middle of the day. The plankton animals died when temperatures reached 42° to 43°C., and were thus often living near their limits of toleration. As a small body of water evaporates, its salinity may become very high. In Italy, Brighenti (1929) studied the animals in the Mesola salt marshes, which reached salinities as high as 41 grams per liter in summer but were nearly fresh in winter. He found a varied fauna which included: ciliates *(Tintinnidae)* and foraminiferans (Trochomorpha). In deeper water were many amphipods, isopods, clams, snails, bryozoans, anemones, and annelids. A few animals ranged from freshwater to the sea—shrimps, anemones, clams, ciliates, etc.; others were found only in the salt marshes. On the coast of California ciliates have been collected in marshes where salinities were 7.5, 12.3, and 20 (Kirby, 1932). After studying the salt marshes of Croisic Labbé (1926) concluded that most of the animals present had come from the ocean, and that some were making progress toward freshwater. In Norfolk, England, a littoral anemone (*Sagartia luciae* Verrill) was found living in water which had a salinity of 14.56 parts per thousand.

Probably because swamps and marshes are often deficient in oxygen, many animals which live in them are air breathers. Especially at night in the tropics the oxygen in shallow water often disappears altogether. This happens because high temperature makes the solubility of gases in water less and because the activities of bacteria and other organisms use oxygen rapidly. In Siam and India there are about twenty-five species of fishes which breathe air and drown if kept under water for from half an hour to two hours (Das, 1927). The snails in swamps in both tropical and temperate regions are commonly pulmonates; whereas those that live in streams, where there is plenty of oxygen, are generally branchiate. Probably lack of oxygen more than the periodic drying up of swamps has made paludine animals air breathers (Carter and Beadle, 1930; Pearse, 1932).

When marshes, swamps, and pools periodically dry up, many of the animals which live in such situations are able to survive. Paludine types are commonly able to burrow, encyst, or go into some other type of dormancy. The ability of the lung fishes to live in a cocoon of mud for months is well known (Smith, 1931). Hall (1901) describes the habits of two eel-like galaxid fishes from Tasmania and New Zealand. These burrow in mud or soil. One swims freely in water, but the other is accustomed to live in mud, swims with difficulty, and dies quickly when submerged in clear water. In Siam aestivating fishes burrow as much as two feet in soil and remain without water for three or four months. When the rainy season comes, serpent heads and climbing perch commonly migrate over the land (Smith, 1927). In Australia there are dragon-fly nymphs which can live in sand without water. Their bodies become so dry that they crackle when handled, but when such animals are put in water they become active in a few minutes (Tillyard, 1917). In Hawaii some dragon-fly nymphs have left the water altogether.

They lurk at the bases of leaves and watch for prey (Perkins, 1897). The phyllopods and certain other small animals that live in temporary pools on prairies and steppes are able to stand great variations in environmental conditions. The eggs of some pool crustaceans will not hatch until they have been dried and subjected to extreme temperatures (Davenport, 1908).

The peculiar combination of variable environmental factors which obtains in marshes, swamps, and pools is conducive to the production of hardly animals and modifications toward land types. Variable temperatures and salinities permit only animals to survive which are able to stand such changes. Lack of oxygen and water makes air breathing and coverings which resist desiccation essential. With these qualities it is not difficult for animals to change from marshy ocean to swampy freshwater or from aquatic habitats to land. Paludal environments apparently have been important highways from sea to land.

Case (1919) believes that tetrapod vertebrates came into existence when paludal conditions obtained over wide areas of the earth. Many palaeontologists agree that bony fishes had their origin in freshwater and that land vertebrates came largely from swamps. "Indeed, it may now be said to be highly probable that although no known genus of lobed-finned fish was the immediate ancestor of the amphibians, yet the group as a whole has the characters to be expected in the descendants of an earlier common stock that gave rise, on the left to the lung fishes, near the center to the known lobe-fins, and on the right to the earliest tetrapods or amphibians" (Gregory, 1933).

SUBTERRANEAN HABITATS

Subterranean animals live where environmental conditions are quite stable. They are in little danger of injury by desiccation; they are not subject to sudden and extreme changes in

temperature; and they are by their mode of life concealed from many predaceous enemies. At times soil animals suffer from lack of oxygen, especially during rainy weather when the water content of the soil is high; sometimes soil reactions change beyond their limits of toleration; but in general they enjoy a considerable degree of stability and safety. They of course have to pay the penalty that nature exacts from all specialists. Their distance perceptive organs, sight and hearing, are often feeble, and they depend largely on contact senses, such as touch, taste, and smell, in their responses to environment. The soil has been invaded by arthropods and vertebrates which come from ancestral stocks which long ago enjoyed an epigean existence. On the other hand, some soil animals such as earthworms, apterygotid insects, tipulid and tabanid fly larvae perhaps spread from aquatic habitats and thus became dwellers in soil instead of in muddy, sandy, or rocky bottoms.

But even along the seashore burrowers are specialists. Certain sponges, worms, echinoderms, molluscs, and crustaceans are able to bore into rock (Russell and Yonge, 1928), and thus find safe retreats on wave-swept shores. Marine burrowers generally attain environmental stability. Reid (1930) found that the water from a freshwater stream which flowed over a sandy beach on the seashore produced no effect on the salinity in the sand below 25 cm. Some worms at low tide burrowed deeper, thus avoided the diluted water, and were able to establish themselves in the estuary of a stream. But fossorial habits always tend to make animals specialists. Marine worms, crustaceans, and clams often have elaborate adaptations for protecting their respiratory cavities (Garstang, 1905) and for breathing in water. Many make characteristic protective tubes of various types.

A few crabs and other crustaceans (Uca, Macrophthalmus, Gecarcinus, Ocypode, Thalassina, Birgus, etc.; Pearse, 1914a,

1929, 1929a, 1931; Verwey, 1927) have quite evidently spread from burrows along the seashore to burrows farther inland, but none of these have become dominant land animals which play an important rôle in terrestrial life as a whole.

The earthworms are probably about the only group of dominant land animals that may have spread from aquatic habitats through the soil. Such careful studies of soil animals as Cameron (1913), Bornebusch (1930), and others have made show that, except for earthworms, dominant soil animals belong largely to modern groups such as Diptera, Coleoptera, and certain Myriapoda. Primitive apterous insects are present in great numbers near the surface and extend down to depths of as much as two meters (Shelford, 1929), but they constitute a very small part of the mass of animals that occurs in soils. It is possible, however, that such minute insects have spread from ancient seashores, as some live in such situations today, and thus have gradually invaded the soils far from water.

A few animals have become established as specialized permanent residents of caves. Certain of the more specialized of these lack pigment, and have degenerate visual organs and enlarged tactual organs. Some of them also occur in underground waters and at times are taken from wells or appear in epigean habitats. Some cave fishes and crustaceans may be said to have rather definite affinities with marine animals (Eigenmann, 1898, 1909; Pearse *et al.*, 1935) and doubtless are relics of a fauna which inhabited the caves when they were submarine or littoral (Davis, 1931). However, the fauna of caves as a whole consists of representatives of rather recent and specialized groups (bats, salamanders, beetles, flies, spiders, and crayfishes), as well as archaic, primitive types. "Temporary residents and some of the less highly specialized cave inhabitants are widely distributed and usually apparently cave forms of long standing. . . . The

nearest relatives of cave animals are nocturnal, or are dark or shade-loving species. Accidents play no part, or at most a very small part, in the origin of cave inhabitants. Animals have reached caves by active migration into places where they find conditions suitable for their existence. Cave species are fitted for cave life before entering caves. Cave species may arise from highly modified animals living outside of caves going directly into the deeper parts of caves, or they may arise gradually by the collecting about the mouths of caves of forms slightly modified" (Banta, 1907). Concerning a recent survey of 41 caves in West Virginia, Reese (1932) says: "Cave crickets and certain Diptera were found in practically all caves; bats in the majority of the caves; fish and salamanders in a few caves. No blind fish were found. Blind beetles were the only blind animals seen." In this case the animals mentioned as being abundant are all recent specialized types.

The soil and the caves included below it contain few animals that have spread from the ocean or freshwater into them. A few such subterranean animals are primitive, but the majority are apparently derived from modern types which have spread from epigean habitats.

DILUTION AND SALATION

Many littoral marine animals are able to live in diluted sea water (Vaughn, 1919; Fredericq, 1922). Such types as the worms of the genera Nereis and Laonice and the king crab, Limulus, will live for weeks in a mixture of one quarter sea water and three quarters freshwater (Pearse, 1928). Some animals (echinoderms) in which the body fluids are nearly isotonic with the surrounding medium are killed when obliged to live in diluted sea water, but others (certain crabs and fishes) can survive gradual or even sudden changes. The hag-fish, a prim-

itive cyclostome, has body fluids which are isotonic with the surrounding medium. "The chloride content of the blood of the hag-fish, *Polistotrema stouti* (Lockington), is comparable to that of the marine invertebrates, and it is probable that part of the body wall of this species is freely permeable to water and salts. This is interpreted as indicating that the hag-fish had no fresh water ancestors" (Bond, Cary, and Hutchinson, 1932).

The waters in the great seas of the earth constitute a great physical-chemical system which maintains more or less stability. Changes in the open sea, except for temporary surface dilutions resulting from rains, are chiefly due to the activities of organisms (McClendon, 1918). In warm seas water is supersaturated with calcium carbonate, and lime is continually precipitated out, largely through the activities of organisms. Ocean water contains a great variety of substances in solution in forms available for use by plants and animals. Marine animals make use of such metals as copper, zinc, iron, and manganese (Phillips, 1932). With the inflowing waters from land areas also come various substances. Among these, compounds which contain nitrogen in available forms are of primary importance. They result to a considerable extent from the work of nitrogenous bacteria, which are largely confined to the land. Because freshwater has average depths that are much less than those in oceans, light should be available more generally for photosynthesis and the initiation of the manufacture of basic foods. But freshwater, because it is shallow, is usually more turbid than seawater, and thus the penetration of light is prevented. When the fundamental needs of the basic activities of protoplasm are considered, there are desiderata in both freshwater and sea water. In the past and at present animals are struggling to pass from one to the other. Usually the chief limiting factor in the productiveness of any area is available food. Nitrogen and phosphorous

compounds are perhaps those which most often are present in minimum amounts and thus limit the manufacture of organic foods, growth, and reproduction.

There are many examples of animals that have been cut off from the ocean and persisted in bodies of water that gradually became fresher, so that they finally became freshwater animals. In the deep lakes in the northern United States (Hoy, 1873), Canada (Adamstone, 1924), and Scandinavia (Ekman, 1920, 1930) there are shrimps (Mysis), amphipods (Pontoporeia), and other animals which belong to genera and families which still exist in the ocean and are looked upon as representative marine animals. Ponds and pools in sandy beaches which have been cut off from the sea remain fresher than the neighboring marine areas, even though they are subject to tidal influences by percolation of water through the sand. Such ponds are inhabited by marine burrowing animals (Calianassa), and such marine fishes as mullets and needle fishes may persist, but, as the ponds grow fresher, they are soon invaded by progressive and aggressive types of insects, such as various Diptera, Coleoptera, Hemiptera, and Odonata (Pearse, 1932). It has been claimed that some lakes, like Tanganyika, have a "marine" fauna (Moore, 1903; Germain, 1913), but "recent discoveries do not favor Moore's hypothesis of a marine Jurassic origin for Tangayika . . . there is no support for the view that the ocean at one time extended over the Congo basin. . . . The view that Tanganyika owes its remarkable organisms to a prolonged period of isolation is regarded as the most likely suggestion" (Cunnington, 1920). Certain blind cave fishes have affinities with marine groups and have apparently remained in cave waters as they freshened (Eigenman, 1909). On the northern border of the Sahara Gauthier (1927) found a species of shrimp in an isolated spring-

fed desert reservoir. He believed this crustacean had been marooned when the course of a river changed.

In many small bodies of water which are cut off from the ocean salinity increases much above that of sea water. In isolated inland pools also evaporation may cause salinity to become very high. In such situations the salts present may differ in character and relative amount from those in the sea. When water evaporates from a salt-containing basin, salts will precipitate out in a certain order; double salts may be formed and separate again when rains dilute the water (Richardson, 1928). In so-called magnesium sulphate lakes in the Caucasus Wornichin (1926) describes three characteristic stages: (1) a period when there is little salt and Ruppia is the dominant plant; (2) a freshening of the water and an increase in Vaucheria and other plants; and (3) an increase in salinity and the formation of felt-like growths of plants. In Devil's Lake, North Dakota, live several species of freshwater rotifiers which have become adapted to life in brackish water (about 1% salt) which is unlike the sea in salt content (Bryce, 1925). Perhaps freshwater animals are less likely to become adjusted to salt water than are saltwater animals to become adjusted to various dilutions. For example, in the Kaiser Wilhelm Canal, which runs from the North Sea to the East Sea and connects with the River Eider, Brandt (1896) found that animals had entered from either end and become established in waters which varied in salt content from 4.7 to 19.0 parts *pro mille*, but only a few stonefly and beetle larvae had come in from freshwater. However, palaeontological evidence indicates that in the past the sea has been invaded from freshwater or from land by bony fishes, pinnipeds, several orders of reptiles, and other animals. Under experimental conditions fishes have been gradually adjusted to water of higher salinity than the ocean. Richtet (1926) kept a fish,

Diplodus sargus (Gmelin), for 7.5 months as the salt content of the medium was raised to 52.1 grams per liter. The fish died when the salinity was decreased to 31.0. In Japan a student working in Professor N. Yatsu's laboratory in 1930 showed the writer specimens of the fish, *Oryzias latipes* (Temminck and Schlegel), which were living in small aquaria in which salinities had been gradually increased. Some had reached salinities as high as 60.0. Certain insects are able to live in high salinities. Ephydrid fly larvae live in the Great Salt Lake, Utah. In Japan the mosquito larvae live in littoral rock pools in salinities as high as 42.0 (Pearse, 1931). At Dry Tortugas mosquito and dragon-fly larvae live in salinities as high as 72.0 and 62.0, respectively (Pearse, 1932e). Animals which live in solutions which contain salts or in solutions which have osmotic pressures which are above or below those of their own body fluids do not vary internally as the surrounding medium varies so that they become isotonic with it. They are animals that have attained some degree of internal stability and thus become more or less independent of the environment (Pike and Scott, 1915; Pearse, 1931, 1932b). There have been many ad- and ab-oceanic migrations in the past and such are taking place today. Animals along beaches in general are able to endure greater variations in environment than those in estuaries and hence more often become established in media which differ from those in which their ancestors lived.

ISLANDS

Islands surrounded by ocean are more or less isolated environmental units which usually have a fauna and flora limited to comparatively few species (Stefani, 1929; Gulick, 1932). Such an area as an island offers is soon invaded by animals which have recently come from the ocean, especially crustaceans such as the crabs belonging to the genera Ocypode and Geograpsus;

terrestrial hermit crabs (Coenobita, Birgus); isopods; and amphipods. The food of such animals is chiefly vegetation and organic refuse (Andrews, 1900; Borradaile, 1903; Pearse, 1929, 1931). Gulick (1932) has emphasized the fact that isolated islands are not populated by land plants, snails, and vertebrates by spreading migrations from the ocean, though he admits that such animals as the gobies that live in Hawaiian streams have come from the neighboring littoral waters. "Really radical new departures seem to require a longer time allowance than these geologically not very permanent islands can furnish." Gulick believes that insular animals such as he discusses are disseminated by wind storms and flight, and to a less extent by transportation on flotsam. The seeds of some island plants remain viable after being immersed in sea water for from thirty to ninety days (Boriza and Bujorean, 1927).

The islands Verlaten and Krakatao, which lie between Java and Sumatra, were covered by volcanic ashes in 1883, and most or all of the life on them was thus destroyed. Dammerman (1922, 1926, 1928) has studied the repopulation of these islands. He observed that the first animals to appear were largely vegetarians and scavengers. A large percentage of these were animals that were able to fly or balloon. Within a few years land crustaceans, land molluscs, earthworms, lizards, and snakes were present. It is possible that life was not completely destroyed on these islands (Sharff, 1926; Becker, 1930), but Dammerman states that the islands were covered with hot ashes to depths of thirty to sixty meters and that no plants or animals could have survived.

Oceanic islands have apparently not played an important rôle in the evolution of land animals from the ocean, but have often furnished habitats which were taken advantage of by animals which could in some way reach them.

LAND ELEVATION

Land elevation and the resulting better aeration of ground water may permit littoral animals to migrate inland through the soil (Harms, 1932). To the writer's knowledge no accurate observations have been made as to what the actual effects of such elevations are. During the great earthquake in Japan in 1923 the shore line at the Biological Station at Misaki rose four feet. Dr. N. Yatsu, the director of the station, states that most of the marine animals which were elevated above their optimum zone soon died and that there was a great decrease in the numbers of littoral animals for several years. A very gradual elevation of a beach might be conducive to the assumption of land life by certain littoral animals. The answer to the question waits for evidence.

Chapter III

CAUSES OF MIGRATIONS FROM SEA TO LAND

THOUGH there is no doubt that most groups of animals had their origin in the ocean and gradually invaded fresh-water and land habitats, there is perhaps some uncertainty as to why animals should leave the stable, dependable ocean and migrate into highly variable situations where life is perhaps more exciting but at the same time more precarious. Some who have considered this question believe that "lures" of various sorts have enticed animals from their ancestral homes (Hesse, 1920), and there appears to be evidence to support such a view. But it is also evident that some animals have been forced to leave the ocean to escape from dangers which threatened racial extinction. Perhaps some also left because of factors which were neither attractive nor repellant.

SPREADING

Probably all species of animals and plants tend to extend their ranges by spreading into all available habitats. Multiplication of individuals leads to overpopulation. In nature various factors operate as checks which keep the numbers of individuals at certain levels. If environment or species change and disturb the existing balance, then numbers may increase or decrease. No matter how specialized an animal may become in its relation to environment, it can never lose its ability to spread. Johnstone (1908) says, "Yet the limitation of habitat is partially compensated for by the evolution of larval stages in the life history of

an organism. We nearly always find that a sessile benthic animal has evolved a free-swimming larval stage; or the primitive pelagic form has evolved a sessile habitat during the latter period of its life history." Even parasites which are securely nestled within favorable hosts at intervals spread into the outside world. Some of them have very special and elaborate means for doing so. Certain parasites are always spread by bloodsuckers such as mosquitoes, ticks, or leeches. To maintain even a small place in the world, a species must have a chance to spread. If this continual pressure to invade new situations is inherent in all organisms, it may at times, when circumstances are especially favorable, move certain animals out of the ocean into littoral, estuarine, or paludal habitats.

SUCCESSION

Organisms invade habitats in an orderly manner. If a new area is opened for colonization, it is generally occupied at first by a few pioneers. These with the progressive physical and chemical changes which occur in all habitats prepare the way for other plants and animals. Then during a transition stage the number of species increases, and an area often becomes thickly populated. Finally certain species which, because they happen to fit the conditions at the particular time and place, become the dominant types and thus constitute what ecologists call a climax formation. When a bit of land sinks below the ocean it is populated in a more or less orderly way by marine plants and animals. The same is true when a portion of sea bottom is elevated into the air, when a landslide denudes a part of a mountain side, or when any environmental change opens a new area into which plants and animals may spread.

Succession and spreading together continually give animals opportunities to explore and occupy new situations. A slight fluctuation in environment may change the course of succession

and lead to a different climax formation. A particular species, if accidentally introduced into an area, early becomes dominant; whereas if it arrives later in the successional series and has to compete with organisms that are already established, it may never be able to do so (Scott, 1910). Succession results in part from the effects of environmental changes, particularly those brought about by the presence of certain organisms which prepare the way for others, and in part from competition between species. Competition and differences in the physical-chemical qualities in habitats bring about the segregation of animals into specific habitats.

SEGREGATION

Animals tend to segregate into groups which become subspecies and in time species. It is generally believed that the ranges of closely related subspecies and species are usually different (Jordan, 1905; Sumner, Cole, and Osborn, 1913; Sumner, 1932), but it is not always so (Richards and Robson, 1926; Pearse, 1933, 1934). This means that competing species usually are not closely related (Robertson, 1906). A group of animals which can find an unoccupied environmental niche escapes certain competitions that its ancestors were obliged to endure. Though subspecies may intergrade along the borders of their ranges, they may be so stable that they will breed true for generations when isolated (Sumner, 1929). New races often originate at localities which are remote from those occupied by the parent stock (Sumner, 1928). Two kinds of changes may be said to take place in animals: (1) geographical, which are often adaptive, and (2) constitutional, which also may be adaptive or not (Crampton, 1925).

In their relations with each other, animals may be individualistic or socialistic, as individuals or as species. They may compete and struggle against each other for things in the environ-

ment, or they may coöperate in such a way as to help each other to survive in the struggle for existence. When two species contest for a habitat one may be better adapted to survive in it than the other and finally dominate. A maladapted species may survive for a long time in a habitat if it is without competition, but, when it competes with species which are better fitted to survive under the given conditions, it soon becomes extinct (Warming, 1909). An animal to survive must continually struggle to overcome environmental resistance, and if its biotic potential is not sufficient to compensate for biological as well as physical-chemical environmental factors which are unfavorable, it cannot survive (Chapman, 1931).

Many animals are especially adapted to avoid competition. Robertson (1906) says, "Species are characterized by noncompetitive habits rather than adaptive structures." Certain plethodontid salamanders segregate most sharply into habitats during their breeding periods. They avoid competition by selecting different humidities, different types of streams, etc. (Noble, 1927). Vestal (1914) has gone so far as to enumerate five types of characters which remove animals from competition: (1) structural, which give animals special advantages in particular habitats (as the legs of a mole); (2) physiological, such as ability to digest and assimilate unusual foods (clothes moth eats keratin) or to exist in peculiar environments (anaerobic animals); (3) psychological, such as preferences for special foods or habitats; (4) biographical, which permit adaptation of life cycles to favorable seasons, feeding to particular times of day, etc.; and (5) numerical by which the numbers of a species are adjusted to food supply or other limiting environmental factors. When a new area is opened for population, competition may be suspended for a time (Borradaile, 1923). Overpopulation may lead to extreme competition, epidemics, and consequent

decrease in numbers. Thus a small group of peculiar individuals may survive the period of stress and initiate a new race or species (Elton, 1924).

Another way in which animals may segregate is through assortative mating (Poulton, 1908). Fulton (1933) recently separated three races of the cricket, *Nemobuis fasciatus* (De Greer), chiefly because they have different songs. These races "are most distinct physiologically than morphologically," and "they seldom if ever interbreed under natural conditions." Probably there are other animals which have formed special groups and taken up life in particular habitats because of peculiar secondary sex characters. "The evolution of secondary sex characters is usually not progressive and continuous but haphazard and often parallel in not closely related stocks" (Noble, 1927). Perhaps it has permitted groups of animals to become adapted to new habitats.

ZONATION AND STRATIFICATION

On ocean beaches all over the earth animals are arranged more or less in zones (Pearse, 1914; Allee, 1923, 1923a, 1923b; Kuhnholtz-Lordat, 1926, 1926a). Such tendencies toward stratification in the distribution of animals in habitats is general, and at times such segregation has apparent relation to differences in temperature, available water, and other environmental conditions. Even among land vegetation there is a tendency for plants and animals to segregate into strata, which begin below the surface of the soil and extend to the tree tops.

Along ocean beaches the tendency of animals to segregate into zones has apparently led to the taking up of life on land by some species. Along the Irish coast the distribution of salt-marsh plants is correlated with the salinity of the water in which they grow (McCrea, 1926). Where mangroves flourish on the

coast of Java the littoral crustaceans are arranged in five rather definite zones through the tidal areas (Verwey, 1930). On the Scottish coast each species of intertidal animal reaches its maximum size at a certain level (Stephen, 1930, 1930a). On the French coast Fischer (1928) has attempted to discover the factors which determine the upper limits of distribution of intertidal marine animals. He finds that exposure of beaches to the open sea may cause waves to distort the zonation which is elsewhere dependent largely on tides. The alga, *Fucus platycarpus* Farlow, and the barnacle, *Balamus balanoides* (L.), have upper limits at mean neap-tide level. "Various other littoral organisms have limits more or less close to high-tide mark or to low-tide mark; almost none stop in the intermediate zone. It is thus frequency rather than duration of immersion that acts upon organisms. Ecological subdivisions may be established in the tidal zone, corresponding to the successive upper limits of distribution of various species."

Prenant and Tessier (1924) have made a very careful study of the zonation of the sessile animals on the beaches at Roscoff, France, and cite the following factors which appear to be most important in limiting distribution: (1) Water level; a few species stand desiccation, but most are continually submerged. (2) Light; some species avoid light, apparently because their larvae are usually negatively phototropic. (3) Freshwater; hydroids and bryozoans have little resistance to dilution; some barnacles have much. (4) Sediment; some species depend on this and organic food in the water. (5) Clearness; some species are limited to clear water. (6) Nature of Substratum; a very important influence, as Alee (1923b) also found. (7) Depth influences, desiccation, wave action, sediment, light, and other factors as well as pressure. (8) Danger, which these authors think is most important of all; most species they find to be arranged according

to this. On the coast of Canada Huntsman (1918a) found that vertical distribution of several littoral animals was limited largely by enemies.

Animals along the shores of all sorts of aquatic environments continually tend to spread into terrestrial habitats but are usually prevented from doing so by various factors. For example, Lieber (1931) thinks that limnodrilids might gradually become land animals if it were not for occasional high waters and frosts which prevent them from doing so. The evidence that many animals have left the sea and attained land life through the intertidal zone has already been reviewed (pp. 15-19). In this section the view is stressed that segregation into habitats, particularly zonation and stratification along beaches, has been a factor in the development of terrestrial animals.

FOOD

All animals require organic food. These they secure directly or indirectly from plants which are able to use radiant energy to manufacture new molecules. A few plants are able to build organic compounds without light, but these are exceptional, and most of the foods consumed by animals result from photosynthesis. As light is absorbed rapidly when passing through water, it is apparent that more energy is available on land for food building by plants than in water. In the ocean and in deep lakes photosynthesis is limited to a rather narrow stratum near the surface. Many streams are so turbid that little light can penetrate them.

Of course a plant requires more than light for the building of organic compounds. Water and chemical compounds which furnish carbon, nitrogen, phosphorus, and other essential elements in available forms are also necessary. Sea water probably contains all chemical elements, but some are present in

minute quantities or unavailable forms. In the ocean there is more organic food near land. In the open sea there is often a scarcity of available carbon, phosphorus, and nitrogen compounds, and such materials are continually added to the sea from the land (Johnston, 1908). On land there is plenty of light everywhere, but the distribution of available water and favorable temperatures is often variable or discontinuous, and some essential elements, such as calcium or iodine, may be lacking. Most marine animals usually live in their food or have it brought to them in the water that surrounds them. Land animals to a greater extent are obliged to seek for foods which remain in particular places (Clark, 1925).

In the past the development of land animals was associated with terrestrial plants, which preceded them and furnished basic foods. The spermatophytes are largely confined to land habitats. Only about thirty species of them live even along the margins of the ocean (Buxton, 1930). Their tissues, and especially their seeds and fruits, furnish water and highly nutritious organic foods in concentrated forms. They have been an important factor in making life for land animals possible (Berry, 1920).

Along the shores of oceans the chief sources of food for marine animals are plants, including minute forms such as diatoms and desmids; organic débris, which may form bottom deposits or travel about in the water itself; organisms brought in by rivers; and jetsam such as accumulates along the drift line. Plant food in the ocean is usually comparatively limited except in cold seas (Harms, 1929). Invertebrate, littoral marine animals feed largely on plankton, algae, or mud, but those which have taken up life on land are generally vegetarians (Borradaile, 1903; Pearse, 1929, 1932a; Watson, 1928). Land vertebrates are often carnivorous (Pearse, 1932a). The intertidal zone

often furnishes an abundance of food and is invaded by both terrestrial and marine animals. In such migrations the vegetarians and scavengers usually precede the carnivores.

There appears to be adequate evidence that various animals have left the ocean in order to take advantage of food resources on land. Along beaches today scavenger crabs which have recently come from the ocean contest for the carcasses of animals along the drift line with terrestrial flies and beetles. In Siam the archer fish shoots insects down into the water where it devours them, certain of the beach gobies run out over the land where they catch ants and spiders (Pearse, 1933), and climbing perch at twilight or during rains leave ponds and streams to search for insects in grassy fields. Various crabs have not left the ocean but continually run out over the land to hunt for food, and some of these (fiddler crabs) probably never seek food under water.

RESPIRATION

There are great differences in the amount of oxygen consumed by various marine animals. Baldwin (1924) gives the following figures, stated as cubic centimeters per gram per hour:

Mackerel	0.726	Nereis	0.291
Scup	0.301	Amphitrite	0.131
Sea bass	0.070	Cerebratula	0.172
Flounder	0.063	Starfish	0.019
Tautog	0.062	Sagartia	0.026
Squid	0.601	Dactylometra	0.019
Phascolosoma	0.367		

At 12°C. the oxygen consumption of the scup was reduced 21%; at 4°C., 40%. In light a scup consumed 0.156 cc.; in dark, 0.115 cc. Evidently more complex and active animals consume more oxygen than do simple sluggish animals.

In freshwater respiration is more difficult than in the ocean, but currents may help compensate for lowered salinity (Prenant,

1929). The presence of monocarbonates in sea water makes the elimination of carbon dioxide easier. This factor alone prevents certain animals from invading brackish water. It is easier for marine animals to invade brackish waters in the tropics than in cooler parts of the earth because monocarbonates are present (Schlieper, 1928).

Most animals require a more or less continuous supply of oxygen and give off carbon dioxide as a result of their metabolic activities. Carbon dioxide may accumulate and be present in such quantities as to be injurious to animals. This seldom occurs in the atmosphere but often does in small, shallow bodies of freshwater, especially if the bottom contains organic débris which by decaying uses up oxygen and produces carbon dioxide. Such animals as rotifers, nematodes, crustaceans, insects, and fishes may be poisoned by large amounts of carbon dioxide in water (Nikitinsky, 1928). On the other hand, many aerobic animals have remarkable ability to live in the absence of oxygen (Dakin, 1925). Fishes are very sensitive to small variations in the gases (O_2, CO_2, H_2S) dissolved in water (Shelford and Powers, 1915). The ability of fishes to extract oxygen from water depends upon the carbon dioxide tension in the water, the alkali reserve in their blood, and other factors (Powers, 1923, 1932).

Respiration is in some respects more difficult in water than air. The atmosphere always contains about 22% oxygen, and poisonous gases are rare. The amount of oxygen in the ocean is quite constant at all depths, but in small bodies of water it may vary from none to perhaps several cubic centimeters per liter. Furthermore, as water grows warmer, its power to hold gases in solution becomes progressively less. In the tropics, therefore, shallow bodies of water often lack sufficient oxygen for the respiratory needs of animals. Bog ponds in temperate

or cool regions of the earth usually contain very little life. This is not only an account of the acids and other substances present, some of which are toxic, but the lack of oxygen in winter when contact with the atmosphere is cut off by a coating of ice (Rigg, Thomson, Lorah, and Williams, 1927; Jewell and Brown, 1929). In the shallow klongs in Siam (Pearse, 1932) and in the tanks in India (Pruthi, 1933) there is little oxygen at night, and many fishes, snails, and other aquatic animals come to the surface to breathe in air. At the mouth of the Amazon River, the lung fish, Lepidosiren, and the air-breathing eel, Symbranchus, live in water that contains very little oxygen and do the same (Cunningham and Reid, 1932). Many river snails are branchiate, but most of those that live in ponds and small streams are pulmonates. Lite and Whitney (1925) studied the development of certain rotifers and found that most eggs develop normally if aerated, but that few will hatch unless they are placed in a decomposing mass of organic material before being aerated, so that the egg shells is broken down somewhat. These animals are thus adapted to conditions which normally obtain in swamps and pools.

A marine sipunculid worm, *Physcosoma lurco* Sel. and de Man, lives in burrows in the intertidal zone between the roots of mangroves, along the shores of the Sunda Islands. It is actively homoiosomotic and typically marine. Because of lack of oxygen in its environment this worm has been forced, according to Harms and Dragendorff (1933) who have investigated it thoroughly, to leave the ocean and live in moist situations or beaches where oxygen can be obtained from the atmosphere. It cannot live without sea water and therefore is confined to the intertidal zone.

Enough has been said to show that the conditions of life in water are such that respiration at times becomes difficult or im-

possible. Animals thus tend to go to the surface where aeration is best or come to depend on the air above the surface for respiratory needs. Some animals, having thus become air-breathers, may wander out of aquatic habitats and finally become terrestrial animals. The respiratory difficulties in water and the advantages in the atmosphere thus contribute to the trend of life toward land.

REPRODUCTION

An animal may live in a habitat where it has an abundance of food, where many other environmental conditions of life are favorable, and where it has few or no enemies, but if proper conditions for reproduction are lacking, the species will become extinct. Many animals leave situations where conditions for feeding and resting are highly desirable and make long migrations to localities where conditions for rearing young are more favorable. Many birds and mammals make annual journeys to particular breeding grounds and spend the remainder of the year where conditions are more desirable for the adults of their species.

The eel spends five to twenty years in freshwater, where it feeds and grows. Then it dons its silvery spawning dress and hastens back to the depths of the ocean to lay its eggs. The young eels spend two to three years in swimming back to freshwater streams and ponds. Salmon, on the other hand, hatch on the pebbly bottoms of cool, clear streams and lakes. After about a year in freshwater they make their way to the ocean, where they feed and grow. When mature salmon migrate up streams to seek out appropriate spawning beds, most species take no food and die after they have shed their gametes. "The stimulus to the performance of the spawning migration is the developing and ripening of the generative organs, and the elaboration of an

internal secretion from the ovary or testis which produces an intoxication, and impels the fish to seek water of definite physical conditions. What these conditions may be depends on the former history of the species—the 'historical basis of acting' being the determining factor in this choice" (Johnstone, 1908). A species' area of reproduction may differ widely from that of its general distribution. An animal's requirements are often quite different at different periods in its life cycle.

In Colombia there is an aquatic swamp snail which always crawls out of water and lays its eggs, like piles of rosy pearls, in bunches on the stems of emergent plants. There are several species of frogs which in similar fashion deposit their eggs in frothy masses so that the young tadpoles when hatching will fall into the water below. The terrestrial marbled salamander long before rains leaves clutches of eggs on land under logs and around litter, choosing situations such that they may be submerged before they hatch (Noble and Brady, 1933). Some terrestrial salamanders have progressed further in their adaptation to terrestrial existence. They pass through all larval stages within egg membranes and are ready for life on land when they emerge.

In progressive adaptation from aquatic toward terrestrial life there is a general tendency to eliminate free-swimming stages in the life histories. Many marine gastropods hatch as swimming larvae; pond snails develop within the jelly deposited by their parents; land snails commonly deposit eggs, which are surrounded by tough shells, in logs or soil, and these hatch into little snails much like their parents. Decapod crustaceans commonly carry their eggs attached to the abdominal appendages. Gravid females of some littoral species run in and out of the water. Some fluviatile and terrestrial crabs do not return to the ocean to breed, but have become adjusted more or less to life in fresh-

water or on land. Many species of animals tend to segregate most sharply into particular habitats while breeding. Certain species of salamanders may often live together but when mating and spawning segregate into different situations (Noble, 1927).

Animals continually seek for suitable breeding sites. This leads such animals as wasps and birds to resort to craggy cliffs; certain birds and seals seek out barren oceanic islands; and other birds fly far to the Arctic barren lands. Animals to attain proper conditions also leave the ocean for freshwater and aquatic habitats for land. Thus they secure safety, aeration, and other desiderata. The seeking of peculiar breeding conditions has been a factor in the development of terrestrial animals.

SAFETY

Animals have often taken up temporary or permanent refuge in freshwater or on lands in order to escape dangers in the ocean. Some littoral animals cannot live below certain levels, or they will be devoured by predaceous enemies (Huntsman, 1918a). Estuaries and swamps have been looked upon by some writers (Hesse, 1920; Annandale, 1922) as refuges where primitive and archaic types may persist after they have been driven from the ocean. Examples of animals cited as those which have thus persisted in freshwater are hydras, certain crabs, and ganoid fishes.

There are marine animals which fear the sea. For example, the fiddler and macrophthalmid crabs which live in the intertidal zone never feed when their burrows are covered with water. They browse about in great armies over exposed beaches, but when the tide rises, each crab retreats into its burrow, plugs up the opening, and remains safe inside until the water recedes again. On rough eroded beaches, like those on the shores of Bermuda and Japan, little snails without shells (Onchidium)

live in the crevices. These never come out to feed when the tide covers their homes (Arey and Crozier, 1921; Pearse, 1931a). The burrowing crustacean which is often called the beach flea (Talorchestia), though it lives a semi-terrestial life along the shore and has little or no toleration for freshwater, avoids the sea (Vervey, 1929). The ghost crab (Ocypode) lives in a burrow on land and commonly hides by throwing sand over its body so that nothing but its stalked eyes protrude (Cowles, 1908). It commonly hunts along sandy beaches at night. If it is then pursued, it may dash into the ocean for a short time but does not stay long. At Tortugas a common predaceous fish, the gray snapper, devours the ghost crab whenever it can.

Johnstone (1908) suggests that salmon were originally marine fishes and that they have developed the habit of spawning in freshwater in order to protect their eggs from marine enemies. On the California coast there is a remarkable smelt, the grunion, *Leuresthes tenuis* (Ayers). This fish comes out on sandy beaches on moonlight nights during March, April, and May to lay its eggs. Just after the highest tides little fishes of this species flop out on the beach above the water, wiggle their posterior ends into the wet sand, and deposit pods which contain about two thousand eggs each. About two weeks or a month later when tides, and perhaps favorable winds, bring high water again the young fishes hatch out and are washed out of the sand into the ocean. "Other smelts lay their eggs very differently, attached to the rocks or the bottom of the ocean by slender stalks or filaments. Many species migrate into brackish or even fresh water to spawn, while other species are entirely confined to fresh water" (Thompson, 1919). The grunion leaves the ocean to find a safe and suitable place for the development of its eggs.

Gobies are fishes which as a group range through a variety of habitats from littoral waters to torrential mountain streams.

Certain gobies are beach slippers. These fishes live near water but show considerable reluctance to enter it. If pursued they skip on top of the water, climb the roots of mangroves, hide among thick vegetation, but seldom plunge beneath the surface or swim (Pearse, 1928b, 1933). The eyes of beach-skipping gobies are adjusted for far vision in the atmosphere, and thus differ from those of most fishes.

Among the enemies that threaten animals in any habitat are parasites. The geographic distribution of parasites and their hosts may be used to indicate the past history and relationships of animals (Metcalf, 1929). Ward (1910) made a careful study of the parasites of various species of salmon in an attempt to determine whether they showed marine or freshwater affinities. He found that European salmon were infested largely with marine parasites, but that those along American shores carried mostly parasites that they had acquired in freshwater. The results were therefore not very conclusive. Trematodes belonging to the family Heterophytidae occur in both the ocean and in freshwater. Stunkard (1930) has shown that some species in this family can complete their life cycles in sea water or in nearly freshwater.

The vermilion spotted newt, *Triturus viridescens* Rafinesque, during its life cycle passes through two phases. In its aquatic phase it carries more parasites than in its terrestrial phase (Holl, 1932). In Japan the parasites of eight species of salamanders were studied (Pearse, 1932f). Some parasites were found only in aquatic and others only in terrestrial hosts. On the whole there was little difference between the two types, except for cases due to host specificity. Acanthocephalans and trypanosomes were found only in aquatic hosts, which may seem natural, but it is hard to understand why opalinid and flagellate parasites were found only in terrestrial types.

At Tortugas the distribution of the parasites of crustaceans was studied (Pearse, 1929, 1930a, 1932c). Most species of parasites occurred in the intertidal zone, but most individual parasites were found in hosts that lived on land. Epistylis, nematodes, barnacles, copepods, isopods, rotifers, mites, and fly larvae occur as parasites or commensals in the gills of crabs. At Tortugas and on the coast of China and Japan (Pearse, 1930a, b, 1931, 1932f) more parasites were found in the gills of land crabs than in those of aquatic crabs, but this was not true at the mouth of the Menam in Siam (Pearse, 1933a), where numerous barnacles lived in the branchial chambers of certain species. In Siam and India more parasites were found associated with aquatic than with land fishes (Pearse, 1932a).

There are many valid instances of animals which have left the ocean to escape various dangers. However, there appears to be no instance where an animal has migrated from the ocean to freshwater or land to escape parasites. Most plants and animals which attack animals as parasites associate themselves with their hosts insidiously. There are some exceptions to this rule. Parts of Africa have been depopulated by tse-tse flies; the caribou migrate north in summer in attempting to escape swarms of mosquitoes and warble flies. Parasites may at times be a factor in exterminating hosts in particular habitats, but they have apparently not played an important rôle along seashores or the borders of bodies of freshwater in causing hosts to change habitats.

TOLERATION RANGES; RESISTANCE

Animals that live along the transition zones between land and water or between saltwater and freshwater are often subject to sudden and extreme variations in environmental conditions, and some of them have become quite resistant to such fluctuations. In their relations to aboceanic migrations the toleration

of animals to certain changes in environmental factors will be considered.

Alee (1923a, b) and Prenant and Teissier (1924) have made rather careful studies of the distribution of littoral animals in relation to environmental factors. Allee, who worked on the coast of Massachusetts, concludes that the character of the bottom is perhaps more important than any other factor. The complex of factors which accompany muddy bottoms are radically different from those which obtain on rocky beaches. Prenant and Tessier made observations on the coast of France, with special reference to sessile barnacles bryozoans, and hydrozoans. They found that the action of strong waves and currents favored the growth of several species of barnacles. Some species endured freshwater well, others did not. One species of barnacle flourished where there was much sediment in the water. Desiccation was fatal to some species but well endured by others. Similar observations were made concerning the tolerations of bryozoans and hydroids. The animals studied by Prenant and Teissier, being sessile, were not such as have been invaders of the land. In fact, few of such types have even attained life in freshwater. The seashore appears to be conducive on the whole to a vast number of individuals of enduring, resisting, unprogressive types. Along with these are a few active, more progressive animals which have generally led the way out of the ocean. Among the latter, ability to stand extreme or varying environmental conditions is one quality that permits the taking up of new modes of life.

It is a primary ecological principle that types of animals which are found in many kinds of habitats have wide ranges of toleration for environmental conditions. The larvae of ephydrid flies live in brine that is much saltier than the ocean; in urine, alkaline solutions, oils, and other media which would be fatal to

most animals. "This ability appears to be due to the presence of a very impermeable cuticle and a very efficient mechanism of hairs and bristles protecting the spiracular openings" (Thorpe, 1931). In the oil vats in California fly larvae subsist on organic food which consists largely of the bodies of dead insects. In the vats their intestines are full of crude oil, which, however, does not come in contact with living cells. Adult ephydrid flies walk about on oil without being injured.

"A characteristic feature of living organisms is the possession of mechanisms which protect them against the effects of changes of their environments.

"These mechanisms in their earlier forms exert their action by restricting the interchange which they allow between the organism and its surroundings. As they develop in efficiency, they become more selective in action, and are able to preserve the essential characters of the organism while allowing a free interchange with its environment. They have preserved, even in the higher organisms some of the conditions of cell life which probably existed at very early stages of their evolution.

"As the complexity of organisms has increased, they have rendered themselves more independent of their external environment by providing their cells with an immediate environment of their own. By this means external changes are only allowed to reach the cells in a modified form. The possession of this internal environment enables the organism to obtain the advantages of a freer interchange with its surroundings without endangering the stability of its essential living matter.

"The evolutionary development of the adaptive mechanisms of the organism has continually extended the range and scope of its control over its environment. . . . As the effectiveness of the mechanisms of the environment to its needs has increased, the

need for further adaptive modification of the organism has correspondingly diminished" (Wardlaw, 1931).

The toleration of animals for variations in salinity, osmotic pressure, gravity, temperature, water, light, food, gases, molar agents, and ionization will be briefly considered in the following pages.

SALINITY

Many animals that had their origin in the ocean can endure salinities below that of sea water, and numerous animals that first came into existence on land have taken up life in the sea. Such typically marine animals as the corals that live in the tropics readily tolerate a reduction of 20% in the salinity of the waters in which they live (Vaughn, 1919). The brine shrimp, *Artemia salina* (L.), may live in water which ranges from fresh to that which is much saltier than the ocean, and its eggs will also develop in a wide range of salinities (Saciacchitano, 1927). Several marine algae live when transferred directly from the ocean to freshwater (Brown, 1915; Chater, 1927). Various worms, molluscs, and king crabs readily withstand considerable dilutions of sea water (Pearse, 1928). The freshwater Rumanian lakes contain a mixture of marine and freshwater types (Borcea, 1931), and the former have apparently slowly migrated in from the ocean.

Finley (1930) studied the survival of fifty species of protozoans when transferred directly from fresh- to sea-water and found that several species were not injured by such treatment. *Tetramitus salinus* (Entz) lives in salinities of 11% to 15%; *Rhizophora salina* Kirby, in 34.8% where the pH is 9.48 (Kirby, 1932). The pulmonate snail, *Physa heterostropha* (Say), remains active in a medium to which sea water is gradually added until the mixture contains 25% of sea water, but becomes inactive at 35 to 40%, and dies in higher salinities

(Richards, 1929). No insects live continually in salinities higher than 2.5%, except dipterous larvae and a larval caddis-fly on the coast of New Zealand (Buxton, 1926), though various bugs live on the surface of the open sea and on the brine in salt vats (Hutchinson, 1931). At Tortugas dragon-fly nymphs survived in water which had gradually grown more salty by evaporation up to more than 6% (Pearse, 1932e).

The aquatic insects of the most specialized groups (Diptera, Coleoptera) are generally more resistant to high salinities than those of more primitive groups (Thorpe, 1927). In the salty ponds in California Diptera occur in the highest, and Coleoptera and Trichoptera in somewhat lower concentrations (Thorpe, 1931). All natural salty waters do not serve as the same type of habitats as sea water, even though their salinities or densities may be similar. For example, a rotifer, *Branchionus mulleri* Ehrenberg, lives in a variety of saline waters including the ocean. Rotifers of this species collected in a pond in Nebraska where salinity was 4.5% thrived in artificial sea water which had a salinity of 3.2% but did not flourish as well as in the same medium which had a salinity of 4.5%. They were little affected by calcium-free sea water and lived in alkaline solutions having salinities of 0.57% to 9.05%. They were unable to live in solutions which contained only one salt (Worley, 1929). In certain African lakes rotifers and fishes were the only animals which were found to live in high salinities or alkalinities (Beadle, 1932a).

Sea-water is a balanced medium, and each ion or radical may have a more or less specific effect on organisms that live in it, or may change the character of the medium as a habitat. Breder (1933) says, "Field and laboratory studies have indicated that Ca has a protective value to marine teleosts against the effects of the lower tonicity of freshwater." Marine fishes have often

invaded waters which contain calcium, even when little sodium was present. Breder tried experiments in aquaria and found that several marine species were able to live in freshwater to which calcium salts had been added. On the other hand, Thorpe (1932) maintains that the general absence of insects from the sea is not due to lack of available calcium. He has found insects in waters where the salinity was higher than the ocean but in which there was little calcium. The Caspian Sea contains more calcium than the ocean and is less saline, but insects have not migrated into it in unusual numbers. Calcium salts in the ocean are important in maintaining the alkali reserve and thus prevent the activities of organisms from producing local acidity (Bruce, 1928). In sea water sodium, magnesium, and potassium as sulphates or chlorides do not affect carbon dioxide pressure materially, but phosphates may do so to some extent, and carbonates have very marked effects (Shelford, 1929).

Respiration in sea water is much easier than in freshwater (Prenant, 1929). The oxygen requirements of freshwater animals are greater, probably because they have to expend more energy in maintaining osmotic equilibrium with the surrounding medium. Changes in salt concentration in external or internal media change the rate of respiration in many marine animals (Schlieper, Borsuk, and Krepo, 1930; Beadle, 1931). In marine animals which cannot adjust themselves to freshwater respiration may decrease or cease altogether in lowered salinities (Shoup, 1932). Carbonates help respiration by taking up carbon dioxide (Harms, 1929).

Aquatic animals generally stand slow better than rapid changes in salinity (Schlieper, 1933). Marine animals show toleration for varying degrees of dilution according to the concentration of the medium in which they have lived previously (Fredereghi, 1931). Such adaptations may exert profound

changes in the whole configuration of an animal. The brine shrimp, *Artemia salina* (L.), has different forms which are correlated with various salinities. Certain littoral snails are smaller in water of greater salinity and larger in lower salinities (Metcalf, 1930). Teleost fishes, in which body fluids are not isotonic with the surrounding medium, change weight and the salinity of their body fluids when the salinity of the surrounding medium changes. Most marine fishes if placed suddenly in freshwater die, probably on account of loss of essential salts (Sumner, 1906; Chassion, 1932) or increased difficulty in respiration (Schlieper, 1929), but a few species are able to survive. Many animals when transferred directly from the ocean into air or freshwater live longer in the former than in the latter (Borradaile, 1903; Pearse, 1929; Barnes, 1932). According to their toleration for varying salinities aquatic animals may be classified as stenohalin or euryhalin (Schlieper, 1933). The former are limited to narrow ranges, and the latter endure various salinities. All animals do not fall sharply into one class or the other (Beadle, 1930a), but there are species or even individuals in a single species which have intermediate tolerations. Nearly related marine species, as the worms in the genus Nereis, may have quite different degrees of toleration for freshwater; young individuals may differ markedly from old individuals of the same species. Some species have narrowly restricted optima; others can change their organization so as to carry on their activities without difficulty through a wide range of salinities. Along the shores of Puget Sound the species of barnacles on the shore indicate the degree of salinity. Some of the species are larger and more definitely divided into zones in high salinities but in low salinities are smaller and less sharply segregated (Rice, 1930). Along the coast of Japan the eggs of each species of oyster require peculiar conditions of salinity for optimum development. Littoral oysters are eury-

halin; brackish-water species are adapted to low salinities; and a sublittoral species is stenohalin (Ameimeya, 1928). Plants along the seashore show rather definite segregation in relation to the salinity of the water (Gessner, 1931).

Reproductive activities are often related to or limited by salinity. The Baltic Sea contains less salt than most oceans. Some adult marine animals are able to persist, but their offsprings cannot mature; others have been favored by low salinity. For example, local species of Nereis and Cyanea have increased in numbers, and Aurelia has decreased (Reibisch, 1926). The eggs of Nereis and other littoral animals may be fertilized and may develop in greatly diluted sea water, but the eggs of such a stenohalin type as Echinorachnius will not survive such treatment (Just, 1928, 1930). Cannon (1923) observed the effects of salinity on the development of a tropical land crab, *Cardisoma armatum* Herklots. He took eggs from a single female and found that in sea-water they hatched into healthy larvae; in freshwater some eggs burst the shell, but no larvae lived; in a mixture of half sea- and half fresh-water some eggs hatched and produced apparently normal larvae. In Siam Alexander (1932) studied the adults of a freshwater crab (*Paratelphusa* sp.). Individuals stood direct transfer from fresh- to sea-water, but died in solutions of sugar which were much below the sea in density. He concluded that electrolytes in the medium were essential.

Many aquatic animals are able to discriminate slight changes in salinity and respond in such ways that they usually survive. Oysters are sensitive to slight variations and cease to feed when salinities fall below certain limits, which are characteristic for each species (Amemiya, 1928; Nelson, 1928). Fishes are quite sensitive to slight changes in the salt content of the water in which they live (Johnstone, 1908; Shelford and Powers, 1915; Wells, 1915). The euryhalin killifish or top-minnow, *Fundulus*

heteroclitus (L.), is able to distinguish toxic from non-toxic salts, but "variations in temperature or in stream flow profoundly influence the reactions and are more powerful factors in the behavior of the fish than the 'presence or absence of salinity'" (Chidester, 1922). Aquatic animals which are placed in solutions that are hypo- or hyper-tonic to the medium in which they have lived may die from various causes. In their ability to resist the effects of changes which may be induced by immersion in fluids which differ in osmotic pressure from those within their bodies animals fall into three groups: (1) those which have external membranes which offer little or no resistance to the passage of water and solutes; (2) those which have semipermeable external membranes that permit water to pass freely but restrict or do not allow solutes to pass; and (3) those which have essentially impermeable external membranes (Pike and Scott, 1915; Hukuda, 1932). Examples of these are: (1) marine invertebrates in which the salt content of the body fluids is much like that of sea-water in which they live, i.e., they are isotonic and isohalin with the surrounding medium; (2) the elasmobranchs (in which body fluids have the same osmotic pressure as sea-water, but contain different salts, and in which the density of the blood is maintained by large amounts of urea) and such animals as earthworms, fishes, and frogs which contain body fluids that differ more or less in concentration and composition from the surrounding medium but are influenced by changes in it; and (3) reptiles, birds, and mammals which differ markedly from the surrounding medium and are little influenced by changes in it (Adolph, 1925).

Death in an unsuitable medium may be due to lack of ability to adjust the body fluids so that they are in equilibrium with the medium, to the toxic action of solutes, to the loss of essential salts, to inability to carry on processes such as respiration which

are essential for metabolism, or to other causes. Hayes (1930) found that Paramecia reared in culture media did not flourish when salinity produced by adding sea water reached 1% or more. "The animals reacted to changes in salinity in at least four ways: alteration in body shape, change in volume, variation in proportion of water, and deviation from normal rate of respiration. The rate of consumption decreased with increasing salinity to the point of isotonicity, after which respiration increased; the curve was thus U-shaped." Quigley (1928) tested the effects of various substances on a shark, *Squalus suckleyi* (Girard), chiefly by varying the proportion of salts present in sea water. He found that the addition of NaCl, KCl, or CaCl to sea water was not very toxic but that "the most toxic solution was sea water with added salts." Cessation of respiration usually occurred before the heart stopped beating. Koidumi (1928) investigated the effects of sea water on certain freshwater chironomid larvae and found that sea water was rapidly fatal, though there are other species of chironomids which regularly live in the ocean. Barnes (1932) studied the littoral terrestrial isopod, *Ligia baudiniana* (Milne Edwards). He found that solutions of single ions commonly present in sea water were toxic in the following order K, Mg, Ca, Na. Rapid death in such a solution as KCl he believed to be due to inhibition of respiratory movements. He concludes that death in dilute sea water is due to the loss of essential salts rather than injurious osmotic changes. Schlieper (1929) has shown that certain marine animals are actively homoiosmotic in diluted sea water, i.e., they work to maintain their body fluids at certain densities by excreting water. In the shore crab, *Carcinas maenas* (Pennant), the intensity of respiration is related to the salinity of the surrounding medium and the crab is able to stand considerable dilution. The shore mussel, *Mytilus edulis* L., on the other hand, cannot keep up

the molecular concentration of its blood in low dilutions and dies, probably from the effects of asphyxiation. Freshwater clams have a low salt concentration in their body fluids, but such salts as they have are essential, and their loss results in death (Ellis, Merrick, and Ellis, 1930). The oxygen consumption of barnacles in air depends upon the salt concentration of their body fluids (Borsuls and Kreps, 1929).

Schlieper (1929) maintains that in freshwater, as well as in marine, animals salinity of blood is related to rate of respiration. When animals are not able to maintain their respiratory activities in changed media they die. Keyes (1931) has studied the survival of the minnow, *Fundulus heteroclitus* (L.) in relation to salinity of water and asphyxiation. He separated his fishes into two groups, those that died quickly and those that lived longer, and found that they differed in metabolic rate. A slow-living fish survives asphyxiation better than one which has a rapid rate; a rapid-living marine fish usually lives in freshwater better. The mechanism for the regulation of such activities is probably concerned with electrolyte equilibria. The oxygen consumption of a marine fish that has been placed in freshwater decreases for a time, but gradually returns to normal if the fish can live. Salts and water leave the body of a fish through its gills in dilute solutions, and the loss of essential salts may thus cause death (Sumner, 1906). In marine invertebrates and elasmobranchs osmotic swelling is proportional to the diminution of the osmotic pressure of the blood (Hukuda, 1932). Changes in weight and salt content take place in teleost fishes when the salinity of the medium varies but are not directly proportional. "The osmotic pressure of the internal medium fluctuates within a much narrower range than that of the external medium" (Sumner, 1906).

Osmotic pressure is like solution pressure of a dissolving solid, vapor tension of an evaporating liquid, or gaseous pressure

of a permanent gas. Each molecule goes as fast and as far as it can. Osmosis exerts uniform pressure in a confined space. It is of course modified by ionization, adsorption, electrical conditions, etc. In a living organism a change in osmotic pressure indicates that work is being done in a cell. The body fluids of animals may be maintained in equilibrium with the environment by the kidneys (Hawthorne, 1930; Schlieper, 1930), or they may be regulated by some other "active living process" (Margaria, 1931).

"The action of all the mechanisms which regulate the chemical relations of the organism is essentially to control the exchange of material which takes place between the organism and its surroundings. In its crudest form this mechanism acts simply by abolishing interchange between organism and environment when the characters of the latter become unsuitable. . . . The differences observable among different species of fish are due to the fact that they possess adjusting mechanisms of different degrees of efficiency and not to the maintenance of specifically distinct levels of osmotic pressure" (Wardlaw, 1931). The changes that animals have undergone to become adapted to various salinities will be considered in the next chapter.

GRAVITY AND MOLAR AGENTS

Gravity is in some respects to be regarded as a factor which is unfavorable to the migration of animals from water to land. The specific gravity of many animals is little greater than that of water. Motile aquatic animals therefore have little difficulty in remaining suspended in the medium in which they live, but those that have taken up life on land live in the atmosphere, and their bodies are much heavier than it.

Terrestrial animals burrow in soil, drag their heavy bodies over the surface of the earth, or have more or less effective and

special means for support and locomotion. If they ascend elevations, they may be subject to injury from rapid falls and violent collisions with the surface of the earth. A land animal must, if it is to attain any degree of dominance in terrestrial habitats, have skeletal and locomotor structures which support it against the pull of gravity and give it ability to move fast enough to compete with other species. A jelly fish can never become established on land. Gravity in a general way limits the size of land animals. Perhaps the ideal terrestrial types are such animals as active flying insects, swift lizards, agile birds, and saltatorial mice. But some types of land animals, like dinosaurs and elephants, have successfully overcome gravity and attained gigantic size. To do this they consume great quantities of food, which has its ultimate source in land vegetation and sunlight.

Gravitational forces are responsible for the tides which exert such a profound influence on littoral plants and animals. The rhythmical ebb and flow of the ocean alongshore alternately exposes animals on beaches twice each day to the influence of the atmosphere and sea water. Intertidal animals therefore develop a certain degree of resistance to the desiccating action of air and the extreme and rapid variations in temperature which are more or less characteristic of terrestrial habitats.

Perhaps some littoral animals have through such influences been transformed from marine into terrestrial types (Flattely, 1920, 1921; Fulton, 1921), but most intertidal animals tend to be radially symmetrical, resisting rather than alert, and unprogressive (Hayes, 1927; Pearse, 1914, 1922) so that few of them through the ages have gone across beaches to land. The tide offers a reward to animals which can establish themselves above high-tide mark. This is the accumulations along the drift line—the flotsam and jetsam of the sea, which furnish food and shelter.

Molar agents in the form of currents, winds, and waves may bring food to littoral animals, transport species to new localities and thus permit them to obtain a foothold, and produce changes in littoral waters which perhaps at times lead to adaptation which help fit animals for terrestrial life. The faunas on wave-washed beaches or on current-swept shores where there are few waves are similar (Fischer, 1927); littoral water in motion has some similar effects, whether it is in the form of waves or currents. The pounding of waves during storms makes it impossible for some animals to live on exposed shores, and the wetting of higher ground by spray at such times makes it possible for marine animals to become established temporarily on land surfaces or in little pools. Where tides are strong they have rather uniform effects on the littoral water in relation to such qualities as content of O_2 and H_2S, pH, salinity, temperature, and turbidity (Miller, Ramage, and Lazier, 1928), but where they are feeble or erratic this is not true (Moberg, 1927). Winds help flying fishes to leave the ocean for short sails through the air, but none of these animals has become established on land. The absence of molar agents may have profound effects on aquatic animals, chiefly through the stagnation of water, which causes animals to die or take up breathing from or through the surface of the water.

TEMPERATURE

In aquatic habitats there are certain inherent advantages and disadvantages that are associated with temperature. As water grows warmer it can hold less gas in solution and more of most salts. Polar oceans therefore contain an abundance of oxygen for respiratory needs and lack available lime, but animals in shallow tropical waters often produce calcareous deposits and at times find breathing difficult. The rate of metabolism in poikilothermic animals is influenced markedly by temperature. An

aquatic animal which lives in a tropical puddle therefore may often lack sufficient oxygen, especially at night when photosynthesis is not replenishing that which is used up by the metabolic activities of organisms. If such an animal gradually becomes adapted to breathing air and is thus able to spend more or less time actually out of water, it meets new dangers in the way of temperature changes, for in any latitude such variations are wider and more rapid on land than in water. Land temperatures, according to Johnstone (1908), may vary between -90°C. and + 65°C.; sea temperatures, -2.8°C. to + 31°C. This gives a range of 155°C. for land and of 33.8°C. for sea. Probably Johnstone's range for the ocean is too limited, but there is no doubt that land temperatures are much more variable than those in water. The specific heat of water is great, and aquatic habitats therefore change temperatures slowly.

Poikilothermic animals live longer at low temperatures, and this fact in part accounts for the abundant populations on the bottoms of some cold oceans and the preponderance of plankton organisms in polar as compared to tropical seas. Oysters live shorter lives at higher temperatures (Hori, 1928). Shelford (1929) has suggested that each type of animal consumes a certain characteristic number of thermal units to complete its life.

The survival or the abundance of an animal in a particular habitat may depend upon the extremes that temperatures reach. Many animals can withstand temperatures below the freezing point of water, but few live above about 40°C. At Naples the death of various marine animals was found to occur at temperatures ranging from 32.5°C. to 43.5°C.; variations probably being due to chemical and physical differences between species (Vernon, 1899). Most animals can change their upper limits of temperature toleration somewhat by acclimatization (Hathaway, 1927). At Tortugas some marine and freshwater animals

live in ponds where temperatures reach 42°C. or more (Pearse, 1932c). On the New England coast high temperatures which intertidal barnacles tolerate range from 23.4 to 27°C. (Cole, 1929). Tropical marine animals live near their maximum limits of temperature toleration, and their activities are readily retarded by cold (Mayer, 1914, 1918). When they die at high temperature it is apparently on account of lack of oxygen to carry on metabolic activities and acidosis.

The faunas of hot springs are derived from freshwater and land. Typically marine animals are absent. "Furthermore the preponderance of species related to ones that have migrated into a marine or semi-marine (brackish) environment indicate that thermal and saline situations have imposed similar obstacles to the biota which has entered them from freshwater. These depend undoubtedly upon the presence of salts in solution and the attendant rise in osmotic pressure of the medium. High temperature is a deterrent that has been overcome by acclimatization ordinarily, however, within quite narrow limits, especially in case of animals, which are able to endure much less heat than plants. An added inconvenience is the rather consistent dearth of dissolved oxygen in thermal waters, which renders respiration more difficult for purely aquatic animals" (Brues, 1927). Most of the inhabitants of hot springs are air breathers. The rat-tailed maggot *(Eristalis)*, for example, is quite characteristic. Its jointed, telescoping breathing tube reaches to the surface and permits the inspiration of air.

There are two types of animals which have left the ocean on account of temperature influences. Some euryhalin animals like the salmon, ciscoes, and certain crustacean relicts, which spawn on the pebbly bottoms near the headwaters of streams (Chidester, 1924) or now live permanently in the cool, profundal regions of deep lakes, are little limited in their environmental relations by

variations in salinity but are associated primarily with cold water. These animals have spread from the ocean whenever there was opportunity. Another group of animals has left the ocean and invaded freshwater to take up life on land in the tropics, where high temperatures make metabolism of poikilothermic animals rapid and thus increase oxygen requirements where the oxygen content of the water is often low and the atmosphere often humid. This combination of factors makes respiration in shallow freshwaters difficult and permits life on land without great danger of desiccation and loss of activity on account of low temperatures.

Adaptations which enable animals to live on land at low or high temperatures may be concerned with bodily temperature regulation, the prevention of water loss, water storage, or the assumption of torpid states. Hibernating insects are prepared for low temperatures by the increase in bound water in their bodies (Robinson, 1928), or, what perhaps amounts to the same thing, a decrease in free water (Bodine, 1923). Mammals also prepare for hibernation by loss of water from their blood (Rasmussen, 1917). Insects survive longest in dry air at high temperatures when they can cool their bodies by evaporation; this means that only insects of some size can live under such conditions, and that small insects are confined to moist, cool situations (Mellanby, 1932). Frogs which have the subdermal spaces full of water can remain some time in the atmosphere, but such a reserve of water is soon exhausted and must then be renewed. A desert lizard is well insulated against the loss of water and adapted to high temperatures.

WATER

Aquatic habitats differ from those on land in that they show no change corresponding to humidity. The ability of many

types of animals to live on land is dependent to a considerable degree on the amount of water present in the atmosphere or soil. Desert animals have special adaptations for acquiring and conserving water.

"The necessity of water in biologic processes is universal" (Rountree, 1922). Water not only furnishes material for building living substance but aids in solution, circulation, oxidation, hydration, hydrolysis, lubrication, excretion, and other activities. Every animal must have a continual supply of water to carry on its life processes. If water cannot be obtained in free form, it must be acquired from food or even by the breaking down of the tissues of the organism that uses it.

Animals along the seashore are adjusted to various degrees in regard to their water requirements. Eight species of snails which Colgan (1910) studied on the Irish coast were arranged in rather definite zones between low- and high-tide marks and showed in the same order progressive ability to survive in dry air; their limits ranging from 6 to 42 days. A mud-flat snail (Ilionassa) from the coast of the United States survived only five days when treated similarly (Dimon, 1905). Two species of beach hoppers (Talorchestia) studied by Verwey (1927) were found to occupy different zones on the beach and to require different amounts of water in the sand in which they lived. Some marine, littoral animals drown in water but must visit the ocean frequently in order to moisten their bodies or their respiratory surfaces. Among these, beach-skipping gobies, fiddler crabs (Uca), and the ghost crabs (Ocypode) may be mentioned. A barnacle, kept out of water for a week or two, goes into a resting state and then will remain alive for some time. Monterroso (1927, 1929) thus kept barnacles alive for from 100 to 140 days. When he submerged them for a short time at intervals of 30 to 90 days, some individuals remained alive for more than

two years. Some barnacles which are attached near high-tide mark are usually submerged for only one hour out of twenty (Flattely and Walton, 1922). The little isopod, *Ligia exotica*, which runs about near the water on tropical beaches may live 8 hours to 4 days out of water, depending on temperature and amount of moisture in the atmosphere. In a saturated atmosphere death occurs when 8% of the body weight has been lost. The body contains about 75% of water, and a loss of 10 to 18% is always fatal. This crustacean must live near the sea because, though terrestrial, it has no special water-retaining adaptations. In Java Harms (1929) found that beach gobies lived only 1 to 5 days on damp mud without water.

Animals that are characteristic of swamps, marshes, and pools often have remarkable powers of enduring desiccation. Water mites stand partial desiccation, if covered with dry débris, for 3 to 6 months, but die quickly if exposed in air (Szalay, 1928). An oriental leech lived in a cocoon on dry paper for a week, during which it lost 80% of its weight, and became active in a short time when again immersed in water (Oka, 1922). Frogs and toads cannot absorb water to any extent from a moist atmosphere, but must come in contact with water, soil, or some other wet object to replenish their body losses (Adolph, 1932). Certain air-breathing fishes in India live without water in moist air on wet grass from 5 to 60 hours (Das, 1927). Collembola on account of their small size are usually limited to damp habitats, but those with tracheal tubes are on the whole able to stand desiccation better than those without (Davies, 1928). Certain serpent-head fishes in Siam remain in dry soil in rice fields without water for as much as four months in stiff mud cells (Smith, 1927). Lung fishes also remain encapsuled in mud cocoons for as long as two years (perhaps sometimes for five

years), and urea may accumulate in their bodies until it amounts to as much as 2% of their body weight (Smith, 1930).

Land animals of course all have more or less ability to do without water and some live their whole lives without any free water. The jerboa and gazelle subsist on vegetation and will not drink if water is available (Buxton, 1923). A fasting meal-worm larva (Tenebrio) can keep its body water constant for a month while fasting at temperatures of 23° to 30°C. and humidities of 0% to 60%. "It seems to be able to do this by consuming some stored substance and holding the water produced in metabolism" (Buxton, 1930). A clothes moth (Tinea) can subsist throughout life on nothing but air-dried wool or fur which contains from 3.66% to 9.08% of water, and maintains its body water at 57.66% to 59.83% (Babcock, 1912). The beetle larva (Trogoderma), which is commonly known as the "museum pest," has lived for more than four years in a small bottle without food, at times molting and devouring its own skin (Wodsedalek, 1917). Argasid ticks may live two to six years as unfed adults, but ixodid ticks usually survive only for six to eight months (Nuttall, 1911).

"The length of time that animals can endure atmospheres of low relative humidity in general depends primarily on the kind of integument and secondly on the proportion of the surface to body mass. Metabolism of an organism is important in its resistance to exsiccation" (Hall, 1922). A man when starved may lose 40% of his body weight, including half of his proteins and nearly all of his glycogen and fat, without serious danger, but the loss of 10% of his water results in serious disorders and of about 20% in death (Rountree, 1922). Shelford (1929) investigated the effects of rapid evaporation produced by air currents, and measured the rate by Livingston porous cups. "The animals killed by rapid evaporation fall into two distinct groups:

(a) those dying with an evaporation varying from 0.07 to 5.40 cc. after an exposure varying from 5 to 165 minutes, and (b) those dying with an evaporation of 31.0 to 42.0 cc. after an exposure of 1,300 to 2,220 minutes. The first group was made up of soft skinned amphibians the second of chitin-covered arthropods. Even though the arthropods were much smaller and hence had much more surface per volume, they lived from 8 to 450 times as long as the amphibians."

RADIANT ENERGY

Radiant energy exerts profound influences on organisms. It produces chemical changes which are injurious to protoplasm; stimulates or inhibits the activity of protoplasm or of whole organisms; makes possible the perception of distant objects by vision; stimulates formation of pigment, colors, and patterns; activates substances in organisms and foods so that they acquire greater value for nutrition and metabolism; stimulates the activity of endocrine glands; energizes photosynthesis; etc. Laurens (1928) points out that light is *visible* radiant energy and that it is a misnomer to speak of ultra-violet or infra-red *light*. A man perceives radiant energy as light which has ranges between 390$\mu\mu$ and 760$\mu\mu$; a honey bee has a range which extends further into the shorter vibrations. The vibrations which are most effective in causing pigment formation in man are about 300$\mu\mu$ in length; still shorter vibrations cause sunburn.

Radiant energy is absorbed as it passes through water in a selective manner. In a general way the longer wave lengths are eliminated near the surface, and the shorter vibrations penetrate deepest. Penetration may be interfered with by suspended matter, surface disturbances, stains, and other things. Seas are usually clearer than rivers and lakes. In a lumber region the presence of tannin in water may cut down the blue light that would normally reach to considerable depths (Shelford, 1929).

Organisms from the ocean may, if they become established on land, gain certain advantages because more radiant energy is available for the manufacture of foods and the furthering of metabolic processes, but they may also suffer from the injurious effects that such energy often produces. In general plants and animals are more or less precisely adjusted to carry on their daily activities in certain ranges. As the radiant energy that is available on the surface of the earth comes largely from the sun and, because of the rotation of the earth on its axis, the supply varies regularly during every twenty-four hours, the activities of many animals are rhythmic. Nocturnal and diurnal animals have energy requirement levels which are adjusted to particular periods in the diurnal cycle. Among common pond fishes in the United States the carp and mud minnow are most often active at night, the pumpkinseed during the day, and the rock bass at all hours (Spencer, 1929). Most locusts sing during the day; katydids and tree crickets, at night. Many cave animals live for generations without light. Even mammals, such as horses in mines, appear to remain healthy for years in the absence of sunlight if fed proper food. Many animals have periods of rest and activity which are correlated with the changes in available energy which occur as the earth travels annually about the sun; i.e., seasonal periodicities. There are many examples of what are known as spring, summer, autumn, or winter animals. Life apparently originated in the ocean where all materials which are essential for the building of protoplasm are available in solution. But energy which may be captured and used to activate organisms is much less in submerged marine habitats than in those on land. It is generally true that the most progressive animals have developed where most energy is available. Kennedy (1928) in discussing insects has made it plain that the most specialized and progressive types are active in the habitats and at the times in

the daily and annual cycles where and when most radiant energy is available.

In struggling to leave aquatic habitats some animals have apparently been stopped by radiant energy. Direct sunlight kills many marine invertebrates (Huntsman, 1924), which therefore must remain submerged or leave their homes in water only at night. On the other hand, some littoral plants and animals which have not been able to leave the salty sea are dependent on the abundant light that is found above the water. For example, the common rockweed (Fucus) can grow submerged or out of the water but must have a considerable amount of light. "Light is the controlling factor in determining the lower limit of Fucus" (Gail, 1920).

FOOD

The advantages of the land in connection with food manufacture have already been discussed (pp. 46-48). In this section it is only necessary to mention briefly the limitations that food as an ecological factor may place on aboceanic migrations.

The food chains, such as that which begins with microscopic floating plants and ends with whales, have been much discussed by oceanographers, and many of them are well known. Most marine animals have a rather stable and ever-present food supply in the water which surrounds them or in the oozy muds which accumulate on the bottom. There are some exceptions to this rule among predaceous marine animals. The black swallower can ingest other fishes which are larger than itself and, as it lives in cool water at considerable depths, probably eats seldom. In freshwater and on land food supplies are more intermittent. Some animals which live in such situations are dependent on foods which may be available only at intervals of days, months, or even years. Correlated with this is the fact that the famous

fasters among animals are to be found in freshwater and on land—leeches, ticks, museum pests, etc. In this connection it is again apparent that animals which leave the stable, dependable ocean to live on tide-swept beaches; in fluctuating rivers, swamps, and pools; or in various land habitats must develop resistances which will carry them through lean seasons. They must at times become torpid and merely endure and at times go without food.

CONCLUSIONS

Animals have left the ocean and invaded freshwater or land habitats for various causes. Some have been forced to leave on account of respiratory difficulties or enemies in water. Others were perhaps attracted by the foods of high quality that are available in freshwater and on land, or by desirable conditions for breeding. Still others left the ocean without any particular necessity or lure in order to escape competition and occupy an unoccupied environmental niche; they became established on land through natural spreading tendencies, as a result of ecological successions and segregations. In attaining land many types have had to give up old racial traditions. They have been obliged to develop new ranges of toleration and new resistances in relation to environmental conditions. They have left habitats with uniformity, stability, and low energy for those in which variability, instability, and high energy are characteristic.

CHAPTER IV

CHANGES IN ANIMALS WHICH HAVE MIGRATED FROM SEA TO FRESHWATER AND LAND

THE view that life originated in the ocean has already been set forth. Some great groups have never left the ocean and are confined to it today—Ctenophora, Brachiopoda, Echinodermata, Polychaeta, Cephalopoda, and Tunicata. Three other groups are largely marine; comparatively few representatives of sponges, coelenterates, and bryozoans are found in freshwater. Amphibia are confined almost wholly to freshwater, but a few frogs even breed in brackish water which may contain as much as 2.6% salt (Pearse, 1911); lung fishes (Dipnoi) are found only in freshwater. Only two classes of animals, Myriapoda and Onychophora, are exclusively terrestrial.

No Protozoa are terrestrial. Though many species occur in soils, they are active only when water is present. Some even occur at times on snow. A few flatworms are terrestrial. They are protected from desiccation to some extent by their slimy secretions, but are confined to moist situations and are nocturnal. Nematoid worms occur in the soil in great numbers. Other species are found in or on terrestrial plants. Earthworms are commonly confined to damp soil, but some of them climb trees and lurk in crevices in the bark. Land leeches commonly rest under fallen leaves or other objects along shady pathways and hasten out into the open when a prospective host passes. Among molluscs only gastropods have attained land life. Many marine

and river snails are branchiate; littoral and pond snails are commonly pulmonate. Land snails lack gills and use the mantle cavity as a lung; they are protected by a mucous covering and, except in slugs, by a spirally coiled shell, which during quiescent periods may be closed by an operculum. They are commonly nocturnal or crepuscular and are active when the air is humid. Their eggs are laid in the soil or in rotting logs and are protected by tough coverings. Arthropods are protected from desiccation by exoskeletons and thus readily take up temporary or permanent residence on land. In Crustaceans which become adapted to terrestrial conditions gills dwindle and organs (tracheae, branchial tufts) develop which permit respiration in moist internal cavities. Excretion through malpighian tubules replaces that through paired metameric kidneys. Insects are dominant land animals and at present share the land habitats with their chief rivals, the vertebrates. Though they originated on land, many have gone into freshwater, and a few types have even become established in the ocean. Noble (1931) has well described the modifications of the vertebrates for terrestrial life as follows:

"If the modern fish were to be changed to a tetrapod, a number of important transformations of structure would have to be accomplished. The gills would have to be lost, and the lungs developed and the nasal passages extended to form internal nares for the ingress of air when the mouth is closed. The fins and body would have to be modified for land locomotion and the integument changed to resist drying. The latter would mean the development of a cornified epidermal covering and a series of integumentary glands discharging by ducts on to the surface, at least over those parts not provided with an armored skin. Special glands would be required to keep the nasal passage and mouth from drying. The eyes, formerly bathed by the water would be especially sensitive to the new conditions and must

either develop a horny, protective cover as in modern snakes or produce softer eyelids out of dermal folds. In either case a lacrimal gland and drain would be needed for cleansing the eyeball. To keep the nasal passage clean a muscular closing device would be required at the outer end of each nasal inlet. If the first tetrapod were to succeed on land, the sense organs of the fish would have to undergo considerable modification, for, while the lateral line organs would be no longer required, the auditory, optic, and olfactory centers would gain a high importance, demanding in some cases fundamental changes in the structure of the organs. If the head were as flat as that of many frogs, special muscles to raise the eyes above the surface of the skull would be needed if the eyes were to be at all efficient. Lastly, the loosely hung jaw of the majority of teleosts would have to be firmly fixed to the brain case."

Land animals have more or less effective, and often elaborate, mechanism for conserving water, regulating temperature, maintaining internal fluids at optimum concentrations, respiration in air, reproduction without water, and locomotion and sensation in air. How such adaptations have developed will be considered in the following sections.

The following classification of animals in relation to environment is proposed by Harms and Dragendorff (1933):

I. Aquatic Animals: positively hydrotactic.
  a. Passively Homoiosmotic, Stenohaline Animals: marine.
    1. Plankton Animals.
    2. Swimming Animals.
    3. Animals Living on Ground.
    4. Animals Living in Ground.
  b. Passively Poikilosmotic, Euryhaline Animals: little adapted brackish water animals. Classes 1 to 4 as under *a*.
  c. Actively Poikilosmotic, Euryhaline Animals: specifically adapted brackish water animals: Classes 1 to 4 as under *a*.
  d. Actively Poikilosmotic Animals, Euryhaline to Homoiosmotic Animals: estuaries and intertidal zones. Classes 1 to 4 as under *a*.

e. Actively Homoiosmotic Animals: freshwater animals, including marine teleosts, dipnoans?, ganoids, selachians, and hemicraniotes. Classes 1 to 4 as under *a*.

II. Air Animals; positively aerotropic.

a. Actively Poikilosmotic to Actively Homoiosmotic. Animals with Well-Developed Skin Organs to Prevent Desiccation (skin glands); in moist (80-90%) air.

1. Flying Animals: e.g., flying frog.
2. Animals Running or Jumping on Ground: amphibians, periophthalmids, coenobitas.
3. Animals Living in Ground: Phycosoma, Lycastris, nemerteans, earthworms.

b. Actively Homoiosmotic Animals with Well-developed Skin Organs to Prevent Desiccation (chitin, horn, imbedded glands): dry air animals which are more or less independent of relative humidity.

1. Flying Animals.
2. Animals Living on the Ground.
3. Animals Living in the Ground.

c. Animals which have Secondarily Returned to Water:

1. Damp Air-Breathers: limnaeids.
2. Animals which have Secondarily taken to Water-breathing: many pulmonates, siphonarians, Ancylus, oncidies, ephemerid larvae.

INTEGUMENT

The chief functions of animal integuments are protection from blows and parasites; insulation against desiccation and loss of heat; respiration; excretion; regulation of body temperatures; and regulation of interchanges between body fluids and the surrounding medium. In general the skins of terrestrial animals are thicker and less permeable than those of aquatic animals (Hesse, 1920; Noble, 1929; Harms, 1930). They thus more effectively prevent desiccation and protect internal organs. Many of the animals that live in the ocean have an integument which permits free interchange between body fluids and the surrounding medium. Some marine animals and those that live in freshwater are able to maintain their body fluids at concentrations which differ from the media in which they live. Certain aquatic animals and most land animals are little influenced by the sur-

rounding medium, even when they are wet continually by rains or immersed in water.

Wardlaw (1931) says, "Far from tending to isolate themselves more completely from their surroundings, the most perfectly adapted organisms are those in which the freest interchange is allowed with the environment." There may be some question as to what "perfect adaptation" means, but there is no question that primitive marine animals in general have freer interchange between internal and external fluids that do more specialized freshwater and land animals. In freshwater it is necessary that liquids be prevented from passing out of the bodies of animals and thus decreasing essential substances, or water must be rapidly eliminated in order to maintain the concentration of internal fluids. Most freshwater animals readily permit the passage of water from their bodies. A paramecium eliminates water equal to 31 to 700 times its own volume daily (Hesse, 1920), depending on temperatures. There are two primary mechanisms involved in the active regulation of osmotic concentration. The kidney concentration of salt and elimination of large amounts of water are characteristic of stenohaline fresh-water fishes; the elimination of excess salt and conservation of the water by the gills appear to be common to the stenohaline marine teleosts and the euryhaline forms like the eel (Keyes, 1933). Chloride-secreting cells in the skin of fishes may keep internal osmotic pressure down (Keyes and Willmer, 1932), and adrenalin, probably by constricting blood-vessels, may decrease or abolish such activity (Keyes and Bateman, 1932). Adult salmon have salt-secreting cells in their skins, but young salmon in freshwater do not.

Protective integumentary structures may manifest themselves as thickenings or special outgrowths such as scales, feathers, or hairs; chitinous or horny cuticle; bony or horny plates; or glands

which form mucus fat, or other secretions. Kennedy (1927) has discussed the advantages and disadvantages of the exoskeletons of insects in a very illuminating way. He says, "The possession of an exoskeleton makes an animal very sensitive to temperature, moisture, light, but at the same time prevents the same animal from developing the more flexible reaction through thought as man knows it. Thought will be forever prohibited to the insect line because it is conditioned on a large mass of properly organized nervous tissue. The exoskeleton of the insect positively prevents the development of a land insect of over an ounce or two in weight." A complete exoskeleton in arthropods is inimical to the development of a large brain. "Besides the skeleton use, it may have developed as an armor in the water or as a protection on tidal beaches." An exoskeleton gives an insect a certain degree of passive resistance, but, as it is a land animal, limits it to a small size and restricts its "reserves of excess tissues." It is stronger than an endoskeleton, gives great surface for muscle attachments, and is excellent for preventing desiccation. The presence of an exoskeleton has left insects plastic in some respects; e.g., it has permitted the evolution of metamorphoses.

Animals such as certain nematodes and dipterous larvae (Thorpe, 1930; Hinman, 1932) are able to live in media which differ markedly from their own body fluids because the cuticles on the outsides of their bodies are practically impermeable. Animals with such cuticles may be aquatic or terrestrial, and the presence of such protective coverings perhaps is to be looked upon as a fortunate accident which permits their possessors to live in media which would be fatal to less protected animals, rather than adaptations which have developed to fit certain environments.

The respiratory functions of the integument in aquatic hab-

itats are served by various types of more or less elaborate gills. Often these are protected in enclosed cavities through which water circulates. Such cavities may enclose the whole body of an animal, as in certain polychaete worms, clams, ostracods, chironomid, and caddis-fly larvae, or merely the respiratory organs, as in shrimps and active snails. In air-breathing and terrestrial animals capillaries are often spread over thin, moist membranes, which cover enclosed branchial outgrowths (Anabas, Birgus, Ocypode) or surround cavities (vertebrate lungs) within an animal. When animals live where oxygen is deficient or difficult to obtain, gills or dermal breathing structures are most often present. Harms (1929) in speaking of beach-skipping gobies makes the generalization that the more a fish lives in mud the more vascular is its skin.

In leaving the ocean for freshwater animals encounter two difficulties which require special abilities or adjustments: (1) respiration is more difficult, and (2) there is danger of loss of essential substances from body fluids to the less dense surrounding water by osmosis. The changes by which the external membranes of animals have been able to meet these will be considered in the next two sections. It is worth while, however, to mention here a few points which bear on the adjustments of the skin in passing from sea- to fresh-water. Such changes have been studied extensively by Adolph (1924, 1925, 1927a, d). No freshwater organism is ever in absolute equilibrium with the environment. Bony fishes in the ocean have body fluids which are hypotonic to sea water. Fishes in freshwater are not very different from those in the ocean, and their body fluids are of course hypertonic to sea water. Marine animals can usually endure variations in the salinity of the medium in which they live better than freshwater animals. The integument may be nearly perfectly permeable and exercise little or no control over the passage of salts, as in a

sea cucumber. Such an animal as an earthworm, a fish, or a frog has some degree of control over the passage of solutes through its skin, kidney, or gill membranes. In earthworms and frogs control appears to be more through the skin than the kidneys (Adolph, 1927a, b).

In migrating from the ocean animals with an exoskeleton or more or less impermeable external membranes have marked advantages over those which can exercise little or no control over the passage of fluids into or out of their bodies. They are able to keep their body fluids in more or less steady state, and their cells continually have a favorable medium for metabolic activities. An animal with a hard or impervious external covering has special advantages on land—the chief colonizers have been arthropods, snails, and vertebrates. The permeability of a tadpole's skin decreases when it metamorphoses into a frog. The skin becomes a better protective mechanism for impeding the passage of solutes. On land it must also retard desiccation. This usually does not facilitate respiration, and breathing in land animals is usually carried on in internal cavities where respiratory membranes may be kept more or less moist without much loss of water.

RESPIRATION

The percentage of oxygen in the earth's atmosphere is greater and more constant than in natural waters. This compensates to some extent for the dangers that land animals endure from desiccation and variable temperatures. It is also true that respiration for an aquatic animal is easier in saline than nonsaline water (Prenant, 1929). This has probably impeded the migration of certain marine types into freshwater.

Respiration is essentially the same process in air as in water, and in the ocean as in freshwater. Colosi (1927, 1930) has emphasized the fact that organisms in passing from aquatic to at-

mospheric media do not change their respiratory medium, since in all terrestrial animals it consists of "a film of aqueous liquid" that moistens the respiratory surfaces and "serves as a path for oxygenation." This "constancy of the respiratory medium" permits migration, during ontogeny or phylogeny, from aquatic to terrestrial environments "without the violent physiological crisis which would accompany an excessive change in oxygen pressure." All organs take their oxygen for respiration from one medium—water. "The physiology of respiration in fishes is the same as in lung-breathing animals" (Powers *et al.*, 1932). In man air which enters at 25°C. and has a humidity of 35%, attains a humidity of 79% in the nose, and of 95 to 98% in the lung (Perwitzschky, 1927). Poikilothermic animals use about the same amount of oxygen per gram per hour as those which live in the ocean at the same temperature (Gjaja, 1922). The rate of metabolism is about the same in reptiles, amphibians, and crustaceans, but in insects and homeothermic vertebrates it is faster (Krogh, 1916). Poikilothermic animals need less oxygen at low temperatures (Helff and Stubblefield, 1929), though many show seasonal variations (Dolk and Postma, 1927). Some poikilotherms, at least, require less oxygen in salt- than in fresh-water (Fox and Simmons, 1933; Schlieper, 1933). The oxygen consumption of barnacles in air depends on the salinity of their body fluids (Borsuk and Kreps, 1931). The alkali reserves in the bloods of animals affect ability to respire in various media. "A series of animals arranged according to their alkali reserve suggests strongly the gradual transition from aquatic to terrestrial life" (Kokubo, 1930).

Marine fishes differ among themselves in ability to live in water containing little oxygen and in respiratory rate. A toad-fish (Opsanus) will remove practically all the oxygen from the water around it, but a scup (Stenotomus) dies of suffocation

when the oxygen tension is still high (Hall, 1929). However, the rate of oxygen consumption of a fish is lowered by a decrease in the oxygen tension or an increase in the carbon dioxide tension of the surrounding water; and a combination of these factors is more effective than either one alone (Powers and Shipe, 1928). Those fishes which can change the alkali reserve of their blood rapidly survive unfavorable gas conditions best. In worms also the rate of oxygen consumption decreases lineally as the oxygen in the medium decreases (Hall, 1931). The rate of oxygen consumption varies in invertebrates (Jordan, 1930; Duryee, 1932) and vertebrates (Hall, 1929) according to the amount of haemoglobin in the blood. However, the rate of oxygen consumption of a fish is lowered by a decrease in the oxygen tension or by an increase in the carbon dioxide tension of the surrounding water, and a combination of these factors is more effective than either one alone (Powers and Shipe, 1928). Those which can change the alkali reserve of their blood rapidly survive unfavorable gas conditions best. In the worms also the rate of oxygen consumption decreases lineally as the oxygen in the medium decreases (Hall, 1931). The rate of oxygen consumption varies in invertebrates (Jordan, 1930; Duryee, 1932) and vertebrates (Hall, 1929) according to the amount of haemoglobin present in the blood.

In many aquatic invertebrates the functioning of gills for respiration is essential for life. For example, if the circulation of water through the branchial chamber of a crab is prevented, death results (Hogben and Zoond, 1930). But there are some aquatic animals, such as may-fly nymphs and caddis-fly larvae, which can live for weeks or months after their gills have been removed (Morgan and O'Neil, 1929; Morgan and Grierson, 1932), though their respiration rate is slower. The land hermit crab, *Coenobita clypeatus* Herbst, lives for months without gills

if kept in air, but dies more quickly in sea water without gills than with them (Borradaile, 1903; Pearse, 1932). The so-called blood gills of certain insects are not always respiratory in function. Those of mosquito and caddis-fly larvae (Morgan and O'Neal, 1930; Wigglesworth, 1933, a, b) appear to be water-absorbing organs.

Many animals that live in water must breathe air and will drown if continually submerged and prevented from reaching the surface. This is true of quite a number of species of fishes. Representatives of some of these are able to wander over land at intervals and in some cases to live for months or years out of water; others never leave the water, and die quickly if they do so. Das (1927), Henninger (1907), Hora (1933), and others have studied tropical air-breathing fishes which possess gills and special organs which are adapted for breathing air gulped in from the surface. These fishes die in from half an hour to four hours when immersed in water. On the other hand, many animals that possess lungs for air-breathing can live if those organs are removed. Krogh (1904) showed that a frog can respire enough through its skin to live after its lungs have been lost. Helff (1929, 1931) extirpated the lungs of frog tadpoles and found that "the young frogs lived for three to four weeks following complete metamorphosis." Yet he also demonstrated that the lungs of tadpoles were functional for a considerable period prior to metamorphosis. The axolotl (Ambystoma larva) survives after the removal of both lungs and gills, its skin being adequate for all its respiration (Hogben, 1926). Some amphibians are peculiarly adapted to live without the lungs, which were doubtless characteristic of ancestral amphibians. Some highly aquatic frogs have reduced lungs (Noble, 1925); salamanders of certain species have no lungs whatever, and their respiration is through enteric membranes and skin. In both these types of

amphibians there is a tendency toward the reduction of the heart from a 3-chambered to a 2-chambered condition by the loss of the left auricle and the loss of the spiral valve. In salamanders with lungs (Ambystoma) the development of lungs precedes that of the auricular septum (Mekeel, 1930). Gage (1892) suggested that in combining adaptations for respiration in water and air animals often retained the former largely for excreting carbon dioxide and the latter for acquiring oxygen.

Aquatic animals in the past have become adapted many times to air-breathing, in or out of water. This has apparently happened most often in marshes and swamps where there was a lack of oxygen and along ocean beaches where tidal rhythms frequently left animals exposed. Fishes may have the swim-bladder adapted for breathing air. In gars (Lepisosteus), bowfins (Amiatus), and some other ganoids the swim-bladder serves as an important organ of respiration. Such fishes are able to live in stagnant water where oxygen is low by gulping air from the surface (Potter, 1927). In a genus (Nemachilus) of Indian loaches the swim-bladder varies in different species in accordance with the need of it for respiration. "In swift currents it is greatly reduced and enclosed in bone; in deep waters of lakes and at high altitudes it is re-developed" (Hora, 1930a). Norris (1892) believed that the swim-bladder of fishes was first developed for respiration and in teleosts secondarily took on hydrostatic functions. The gills of fishes, though often covered by opercula, are in a sense "open" organs of respiration, but swim-bladders, lungs, and other similar organs for air-breathing are in a sense "closed" as they enclose internal cavities (Powers *et al.*, 1932).

Fishes have become adapted to air-breathing in diverse and peculiar ways. Gobies which skip about on muddy ocean beaches have the adductors of the gill arches poorly developed; the

epithelia of their gill filaments show more mucous, cornified, and albumen-secreting cells, and thus desiccation is inhibited; gill surfaces are reduced; the skin, buccal, and branchial epithelia may serve for respiration; in some species there is a cavity above the first gill; the mouth is small; the opercular aperature is narrow (Schöttle, 1931). Young land gobies have gills like aquatic gobies, but these change with other features during metamorphosis. In modern gobies and blennies "skin respiration is improved by the penetration of capillaries into the epidermis. An extreme saccular enlargement of the buccopharyngeal cavity increases the efficiency of buccal respiration. Gulped air is prevented from escaping through the gill slits by a modification of the gill covers" (Noble, 1931).

Bridge (1904) and Rauther (1910) have described the various types of air-breathing which occur in fishes. Their lists include the skin; air bladder; expansions from the buccopharyngeal cavity; labyrinthine organs contained in such cavities and mostly developed from gill arches; lung-like growths from the pharyngeal cavity; and vascular intestines aerated by bubbles taken in through the mouth. There has been no uniformity in the development of such organs in particular groups of fishes. They therefore appear to be of independent origin. For example, the silurid fishes show three or four different types of air-breathing organs. Carter and Beadle (1931) in their investigations in the tropical swamps of the Gran Chaco found four types of air-breathing organs in fishes: (1) lung-like air bladder; (2) large gill chamber without special structural adaptations; (3) vascular intestine with contained air bubbles; and (4) vascular stomach with contained air bubbles. They give a list of all air-breathing fishes in the world, with their types of adaptations.

Amphibians furnish an interesting series of types ranging from those which are aquatic in all stages in their life cycles

(Siren, Necturus) to those which are completely terrestrial (Plethodon). Many begin their lives in water as tadpoles and metamorphose later into land animals. The American newt, *Triturus viridescens* Rafinesque, may remain aquatic throughout its life (Noble, 1929) or spend two or three years on land, and then return to the water to breed. "The subjection of the incompletely metamorphosed newts to terrestrial conditions causes a reduction of the gill stubs. . . . Siren is a form which has ceased to differentiate most of its structures beyond the stage characteristic of the early larva" (Noble, 1929). Morgan and Sondheim (1932) found that keeping gilled newts in a dry environment caused no reduction of gills, but the transplantation of portions of anterior pituitary lobe into the bodies of animals induced both males and females to become sexually mature though still bearing gills.

A frog tadpole is in a state somewhat comparable to an adult dipnoan. According to Willem (1920), a frog passes through five stages in regard to its respiration: (1) tadpole with internal gills like a fish, (2) tadpole with perforate nostrils and buccal respiratory movements, (3) young frog depending on cutaneous and buccopharyngeal respiration, (4) terrestrial young frog still dependent upon cutaneous and buccopharyngeal respiration, and (5) a frog dependent largely on lungs but still using skin when necessary. Certain salamanders that live in brooks and on land have no lungs and depend on buccopharyngeal and cutaneous breathing. The cutaneous respiration of a frog is not under the control of the nervous system, but pulmonary respiration is (Krogh, 1904). Certain African tadpoles (Hoplophryne) which live on bamboos and banana plants hatch with functional lungs. They never develop external gills, and their internal gills are rudimentary (Noble, 1929a).

The changes in respiratory organs which have fitted animals

to live on land have among fishes and amphibians been largely developed in connection with migrations from freshwater to land, but among crustaceans there are many examples of such modifications associated with migrations across ocean beaches, directly from sea to land. Littoral hermit crabs (Paguridea), arranged in order from deep-water to terrestrial types, show a progressive reduction in the number of gills (Fig. 1). Littoral crabs (Brachyura) in a similar fashion show a progressive reduc-

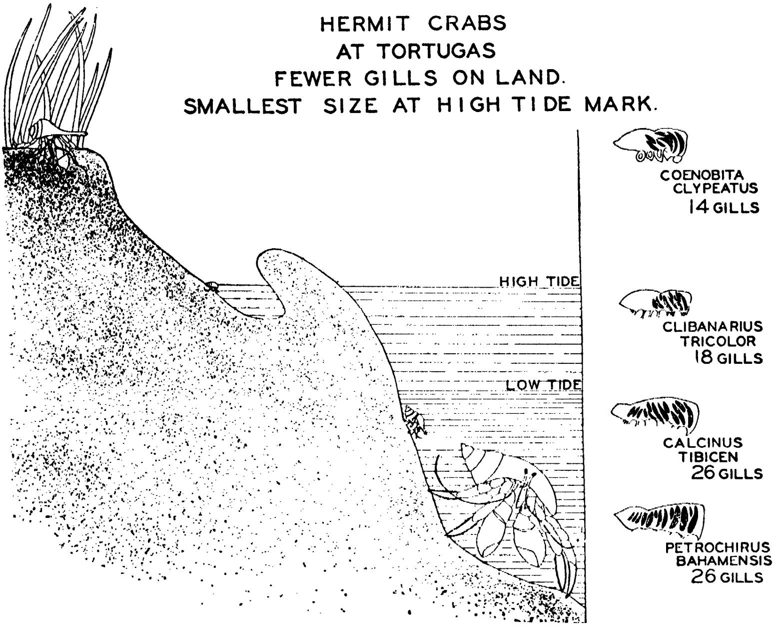

FIG. 1

tion in gill volume in relation to body volume (Fig. 2). At Tortugas and on the North Carolina coast a littoral aquatic crab has a body which is about twenty times the volume of the gills, but in a land crab the body has sixty times the volume of the gills (Pearse, 1929, 1929a). A land hermit crab will live several months after its gills have been removed (Borradaile, 1903; Pearse, 1929). An intertidal crab (Uca) may carry water in its

branchial chamber. "The fiddler crab is a true water-breathing animal, but it can live in the air for several weeks without changing the water in the gill-chambers" (Dembowski, 1926). Barnacles, on the other hand, though bound to the ocean forever by their sessile mode of life and method of feeding, are terrestrial rather than aquatic animals in their respiration (Monterosso,

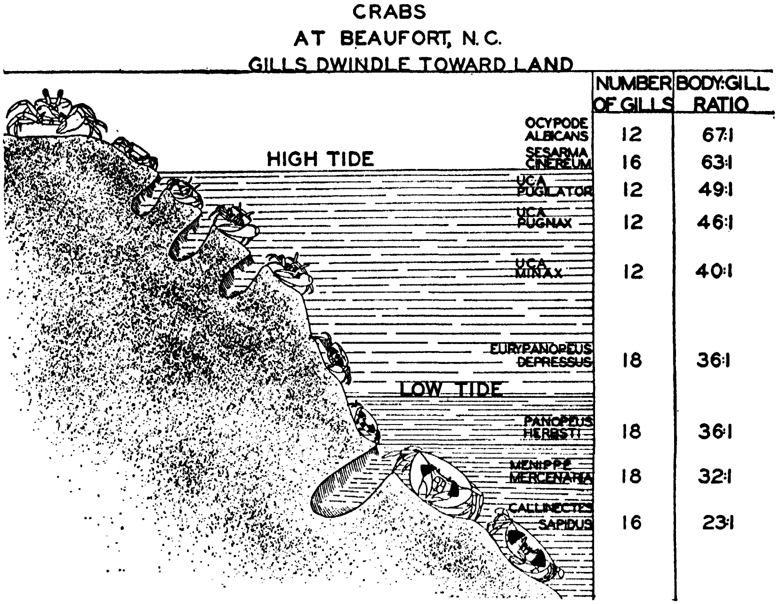

FIG. 2

1927). Verwey (1930) has classified littoral crabs according to their methods of respiration as follows:

I. Water Crabs with Large Inhalent Opening: portunids such as Scylla, Neptunus, Thalamita.

II. Transition Breathers without Large Inhalent Opening:
  1. Pumpers: Pump water out of branchial chamber. Sesarma, Ilyoplax, Metaplax, Macrophthalmus.
  2. Non-pumpers: Circulate air through water in branchial chamber.
     a. Having normal course through branchial chamber. Grapsus, Potamon.
     b. Having special respiratory openings between 3 and 4 legs. Uca, Ocypode.

There are land crabs (Gecarcinus, Cardisoma) which do not carry water in their gill chambers, and the respiratory cavities of Oypode are not completely filled with water (Pearse, 1929).

As aquatic crabs take up life on land, various changes take place in their respiratory organs (von Raben, 1934). Often the gill cover takes on greater respiratory functions and in some cases becomes quite vascular, even developing lacunar systems which are surrounded by capillaries. The chitinous covering of the gills tends to become thicker. There are mechanisms for keeping the gill plates moist; in some cases water passes from the mouth through a special canal to the gills. Some land crabs breathe through vascular areas on the abdomen.

Marine molluscs are for the most part gill-breathers, but a few littoral species have become air-breathers. River snails are commonly water-breathing, but in swamps and marshes air-breathing is the rule, and land snails are generally pulmonates.

Annelids which live in tubes or in stagnant water often develop gills, which are commonly evaginations of the skin. In the swamps of the Gran Chaco, Carter and Beadle (1931a) studied methods of respiration in eight species of oliochaetes. They do not believe that any of these worms can live anaerobically, but that all are able to endure low oxygen contents in the medium in which they live. One Aelosoma lived in the narrow oxygenated surface stratum, building a tube attached to plants. One large species (Drilocrius) burrowed in mud in shallow water. It was found to have a groove on its back in which it carried down a bubble from the surface.

There is abundant evidence from the past and present which indicates that air-breathing originated on beaches and in stagnant water long before life developed on land (Pearse, 1930, 1932b). Hall (1924) believes that primitive cartilaginous fishes (Chondrostei) used vascular enteric membranes for breathing from air

that they had gulped in. One line of development (Holostei, Teleostei) from these emphasized the swim-bladder as a respiratory-hydrostatic organ, and another line (Crossopterygii, Dipnoi, Amphibia) developed a lung. Hall also points out that toads have improved their lung as an organ for use on land over that of aquatic salientians by enclosing the alveolar sacs more completely, so that they better conserve water. Reptiles have further isolated lobules by the development of branching bronchi. "The respiratory organs of terrestrial vertebrates are lungs. These arose in phylogeny long before the land was invaded" (Noble, 1931). "Aerial respiration was apparently first achieved by ganoid forms higher than the elasmobranchs, but ancestral to the Crossopterygii and Dipnoi. . . . A lung in the form of an air bladder opening off the ventral surface of the esophagus was present in the early ganoids before the line leading to the early Dipnoi, the Crossopterygii, and the Amphibia was separated from the parent stem" (Smith, 1931). A primitive type of lung persists today in the Dipnoi. "The breathing of atmospheric air had already been acquired by several groups of fishes of the ancient coal swamps, as it has by several unrelated modern fishes. If we may judge from modern conditions an oxygen-secreting pouch long served to tide the fish over periods of drought, and possibly the stout fan-shaped paddles assisted them in wiggling from one pool to another. When breathing by the air-sac finally superseded breathing by gills, in the adult stage, it is not surprising that the opercular bones, which play an important part in branchial respiration, should have failed to ossify, leaving only a dermal flap. The region of the otic notch in Amphibia corresponds closely to the opercular flap in fishes" (Gregory, 1933). Morris (1892), Spengel (1904), Ballantyne (1927), Goodrich (1930), and others have discussed the origin of lungs.

Pike (1924) has reviewed the changes in vertebrate respir-

atory mechanisms. The appearance of lungs necessitated the development of new respiratory muscles. Coördination between swallowing and breathing was necessary. At first the body wall functioned for breathing. A reptile could live out of water. It might swallow in a leisurely way and breathe at the same time. A mammal with a diaphragm did even better. New nervous and muscular mechanisms made possible the methods of breathing which are now correlated with the rapid metabolism of homeothermic animals.

BODY FLUIDS

"The first living forms had the sea for their environment. Every cell, doubtless, came into contact with this fluid which was at the same time the source of its food and oxygen supply. As cells began to be associated in smaller or larger masses, channels were left between them through which the water of the sea might find passage. Animals a little farther along the scale of development shut off their body cavities, vascular and otherwise, from direct communication with the sea, but did not succeed in freeing the cells from the necessity of getting their food and oxygen supplies by diffusion from a solution. The fluid shut within the animal body furnished the immediate environment of the cells; it took the place of the sea in the economy of the organism. It has been seen that the fluid becomes more and more complex in structure as one passes in review from lower to higher forms. And while the internal fluid sea, bathing the individual cells, has become in some respects more complex and able to play a greater variety of functions in the life of the organisms, there are certain features in which it harks back to the primitive conditions which must have existed millions of years ago" (Rogers, 1927).

The salt systems which bathe the living cells of animals in

which body fluids differ from those in sea water do not have the same proportions of salts as occur in the ocean. Those in freshwater animals of course differ markedly in salinity and composition from the surrounding medium. However, as Dakin (1912) has pointed out, an aquatic organism is not a closed system which is independent of changes in its environment. Such changes may affect internal media physically or chemically. The bloods of marine animals may differ markedly from those in the surrounding ocean. The salts in siphunculids and starfishes are about the same as those in the sea; but the quantity of those in crab and snail bloods are always at least a little below; and those in fishes are much less and rather constant (Duval, 1924, 1925). On the whole, the blood of many marine invertebrates is much like the ocean, but vertebrate blood substances always differ from the surrounding medium. "Marine invertebrates which have invaded brackish and fresh waters often present an independence of the blood which is not at all unlike that of vertebrates. For example, in both the freshwater crayfish and a frog immersed in water, there is a constant controlled diffusion inwards of water and a regulated output from the excretory organs. A new freshwater crab (from a river in New South Wales) with which we have been experimenting retains a constancy of blood salinity which is less than half that of the ocean from which it undoubtedly wandered, yet its sojourn in freshwater cannot have been of long duration" (Dakin, 1931).

The salt content of freshwater is not only less than that of the ocean but differs in composition. "In striking contrast to these [sea] solutions, in which sodium is 30 to 50 times more concentrated than the calcium, are the dilute salt systems in which avascular freshwater animals are found. Two salient characteristics emerge from a review of a number of analyses of different freshwaters: (1) they are much more dilute than the

blood of higher forms, being about 0.01 per cent total salt; (2) the calcium is quite generally more concentrated than the sodium and the potassium together" (Hetherington, 1932). Marine animals which attempt to enter freshwater usually are not killed so much by dilution as by loss of essential salts (Sumner, 1906; Adolph, 1925; Hill, 1931). A conger eel may survive for days in 0.1 sea-water but dies in a few hours in freshwater (Hill, 1931).

Sea-waters and bloods are complex systems which contain salts, organic materials, colloids, ions, and other substances which may affect organisms. Each substance probably has more or less specific effects on protoplasm and vital processes. Some marine animals contain more than 99% water in their bodies (Gortner, 1933). Others commonly maintain body fluids which contain such mixtures of salts and organic materials as to make them slightly denser than the sea-water. Other marine animals maintain their body fluids in a steady state which is much less dense than sea water. Three types of equilibria occur in animals, and these represent different osmotic relations with the environment: (1) body fluids are isotonic and isohalin with the external medium; (2) body fluids are isotonic but not isohalin with the external medium; and (3) the body fluids differ in osmotic pressure and content from the external medium, and are therefore more or less independent of environment (Fredericq, 1922). Representatives of all these types live in the ocean today. In animals osmotic pressure cannot rise much above that of the environment (Shelford, 1929), but in plants it may be two or three times as great (Atkins, 1917). It has been suggested by some that the low and more or less stable osmotic pressures that are characteristic of vertebrate blood are survivals of conditions in primitive seas which had an osmotic pressure of perhaps a third what it is today (Wardlaw, 1931); but such arguments are

made questionable by the fact that bony fishes appear to have had their origin in freshwater (Barrell, 1916; Case, 1919), though the remoter ancestors of fishes were probably marine. Blood is not derived from the waters of old oceans but from the body fluids of the inhabitants of those oceans (Dakin, 1912).

As animals left the ocean to invade freshwater and land habitats, there were changes in the character of limiting membranes and the body fluids. In animals there are two lines of defense, so to speak, where changes may be permitted, controlled, or prevented: the membranes on the outsides of bodies and those covering cells which may lie deep in the interior. In protozoans and sponges there is little distinction between these, but in metazoans which have inclosed blood and lymph systems the distinction is marked. In aquatic animals the permeability of the external membranes is of primary importance. Many marine animals permit all constituents of sea water to pass in and out of their bodies. Changes in the osmotic pressure of external media in general limit the distribution of freshwater animals more than those of marine animals. In gaining ability to retain salts in hypotonic media the latter have apparently lost ability to adjust to changes (Adolph, 1925). A frog tadpole at the time of its metamorphosis undergoes marked changes in regard to the ability of its skin to resist changes in the osmotic pressure of the surrounding medium (Adolph, 1925, 1927a, b). An adult frog apparently has a mechanism in its skin which is under nervous control and which regulates somewhat the passage of water and solutes (Adolph, 1933). There is general agreement that animals which have gained ability to regulate or resist diffusion processes through their external membranes have done so by the addition of controlling mechanism. An animal that maintains a dynamic steady state during which its internal fluids differ in osmotic pressure and composition from those outside must

continually do work (Adolph, 1925; Pantin, 1931; Hill, 1931); the regulation is not merely diffusion but an active process carried on by living tissues.

Beadle (1934) has studied a flatworm *(Gunda ulvae)* which lives where it is alternately subjected to water from streams and from the ocean. This worm can live permanently in any concentration of sea water down to 5%. It is able to maintain a relatively constant internal state against a rapidly changing external environment. When it is transferred to dilute sea water there is an initial flow of water through the integument into the parenchyma, which causes swelling and a temporary lowering of activity. The water is soon taken up by the gut, and forms intracellular vacuoles. This process requires an expenditure of energy, as it is inhibited by cyanide. The parenchyma soon returns to its original condition and resumes its normal activity. Then the animal sets up a resistance, and the integument becomes less permeable, but the gut remains vacuolated as long as it is in dilute water. The excretory system does not appear to be concerned particularly with such regulatory processes. "Distinction must be drawn between the ultimate impermeability of the ectoderm considered as a membrane and the osmotic resistance of the individual cells of this layer and of other tissues. The permeability of the ectodermal membrane can be reversibly increased by calcium deficiency, but the osmotic resistance of its individual cells cannot be broken down by this means." Both the vacuole formation by the gut and the osmotic resistance developed by individual cells are believed to be active processes which expend energy, but the impermeability of the external membrane is a passive process.

The salinity of body fluids of animals is influenced chiefly by three factors: (1) the external membranes, (2) the products of metabolism present in the internal medium, and (3) the renal

organs (Dakin, 1912). In freshwater the bloods of crustaceans generally have higher salinities than those of molluscs. Such differences are inherent and dependent on characteristic racial adaptations. In the ocean the salt content of the bloods of sharks and bony fishes is similar. But the blood of a shark is isotonic with sea water, its osmotic pressure being maintained by the presence of large quantities of urea, while that of a teleost has only about a third of the osmotic pressure of sea water. European littoral crabs present a graded series in regard to their ability to maintain a constant internal medium: the blood of

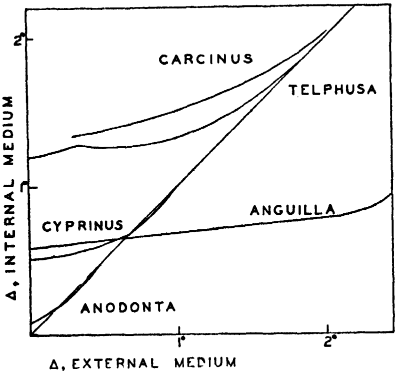

FIG. 3. The relation between molecular concentration of the blood and that of the external medium in various aquatic animals: *Anodonta* sp., *Carcinus maenas*, *Telphusa fluviatile anguilla*, and *Cyprinus carpio*. After Schlieper (1933).

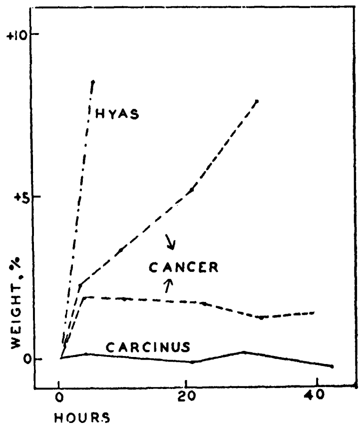

FIG. 4. Change in weight of *Hyas aranea*, *Cancer pagurus*, and *Carcinus meanas* after transfer from the North Sea (salinity, 3.2%) to brackish water (salinity, 2%). After Schlieper (1933).

Hyas rapidly becomes isotonic with sea water or dilutions of it which surround its body; Cancer changes much more slowly; and Carcinus is little influenced by changes in the salinity of the water around it. When placed in diluted sea water Hyas absorbs water and increases in weight rapidly; Cancer changes more slowly, and some individuals change very little; Carcinus does not change (Schlieper, 1929, 1933). Crustaceans, in order to attain equilibrium with the surrounding medium in dilute solutions,

excrete water largely through the kidneys (Schlieper, 1933), but fishes lose water chiefly through their gills and other external membranes (Dakin, 1912).

A freshwater clam has little ability to resist osmotic changes in hypertonic solutions, and dies rather quickly in salt water (Fig. 3), but a crayfish is more hardy. The former has little salt and little organic matter in its blood; the latter has much of both. A crayfish heart when perfused with various solutions continues to beat through a wide range of molecular concentrations (pH 5.5 to 9.0; Lindeman, 1928). In Siam Alexander (1932) studied a freshwater crab, *Paratelphusa sinense* Milne Edwards, which survived immersion in sea water (pH 3.0 to 10.0) for four hours.

Perhaps the most primitive function of bloods in animals is that of furnishing bodily tissues a solution containing the salts necessary to keep cells in a physiologically balanced condition. Other primitive functions are the carrying of nourishment and materials needed for metabolic processes, as well as the wastes resulting therefrom. The transportation of hormones, antibodies, leucocytes, and other protective substances is also done by circulating body fluids. Many bloods produce clots which effectively plug up holes produced in the bodies of animals by injuries.

As animals progress from ocean to land, their bloods are on the whole less saline (Pearse, 1931, 1932b; Rogers, 1927, p. 148) and more stable. Salts, which in primitive animals are like those in the sea, become specific in quantity and function. They keep internal media which bathe living cells constant by acting as buffers and preventing acidity through combinations with the products of metabolism. More lactic acid is secreted in the active muscles of land vertebrates than in those of aquatic

animals (Ritchie, 1927). Alkali reserves which combine with carbon dioxide or other substances become subject to control by internal mechanisms and are increased when such changes as decrease in oxygen or increase in carbon dioxide occur in the environment (Powers and Logan, 1925). As blood functions increase and become more specific, blood cells become specialized as phagocytes, antibody producers, oxygen carriers, etc. Blood pigments, which perhaps first occur as inert waste products, come to serve important functions as oxygen carriers. They may be present in the plasma or confined to particular cells or corpuscles. Haemoglobin occurs in vertebrates in corpuscles, except in the lancelets in which it is plasmic. It is also found in various crustaceans, insects, molluscs, annelids, gephyreans, echinoderms, and nemerteans. Haemocyanin is found in various crustaceans, arachnids, gastropods, and cephalopods. Other respiratory pigments are found as follows: chlorocruorin, chaetopods; haemerythrin, gephyreans; chlorophyl, lepidopterous insects; and tetronerythrin, decapod crustaceans. The occurrence of respiratory pigments is without reference to phylogenetic relationship. Some chironomid larvae which live in stagnant water contain so much haemoglobin that they have long been known as blood worms; others which dwell in well-aerated waters are quite transparent. It has been said that haemoglobin occurs where there is a dearth of oxygen; often in aquatic habitats on account of a deficiency in the environment and often in aquatic and terrestrial habitats where an impervious external covering or a large body make the carrying of sufficient oxygen to internal tissues difficult.

Body fluids as animals were gradually transformed from marine to freshwater, and land animals changed from sea water to comparatively dilute, exactly regulated, viscous, nutritious,

corpusculated, and pigmented liquids. Instead of furnishing merely suitable media for bathing living cells, they have come to serve a variety of functions concerned with nutrition, respiration, excretion, the humoral control of activities, and the prevention of damage from disease or injury. The history of the rise of land animals has been a bloody one. Emphasis has shifted from dependence on a primitive dependable external medium to that on a specialized, highly regulated internal medium.

METABOLISM

The quality of metabolism in all animals is apparently similar, but the rate varies markedly on account of inherent hereditary qualities and because of variations in environment. Size has a marked influence on rate of metabolism on account of surface-mass relations. A man to keep his body warm must expend food equal to about 1% of his body weight each day; a mouse, 25%; and an insect, if it were to maintain the same temperature as a mammal, 625% (Kennedy, 1927a). It is apparent that an insect must continue to be poikilothermic, and can be active therefore only when its environment is warm. Animals consume about the same amount of total energy per gram during their lives (Rubner, 1924b). Smaller animals live faster, shorter lives than larger animals. Rats live twice as long if prevented from exercising as when they exercise, because they expend energy more slowly (Slonaker, 1926). The longevity of many poikilothermic animals is more or less directly related to rate of metabolism, as determined by temperature (MacArthur and Baille, 1929).

The most active marine fishes have most haemoglobin in their blood and carry on metabolism at a high rate; sluggish fishes are better able to utilize oxygen when it occurs in low concentrations, and to endure lack of oxygen (Hall, 1929).

Rate of metabolism has apparently not been an important factor in the migration of fishes from sea to freshwater or land, but it has been for many invertebrates. For example, the respiratory rate of crabs varies more or less with the salt concentration in the surrounding medium. This happens because the rate of metabolism depends somewhat on the amount of osmoregulation required (Schwalbe, 1933). Many marine invertebrates cannot increase their energy utilization in freshwater and therefore perish. Some, however, are able to make temporary or permanent adjustments to waters of low salt concentration. The kidneys of shrimp of the genus Palaemonetes and of other crustaceans vary in structure according to the salinity of the medium in which the animals live. The thyroid gland of vertebrates produces a hormone, thyroxin, which increases metabolic rate. "It seems the business of the gland to maintain in the blood a certain definite though small concentration of an iodine compound. In doing so it may, as has been suggested, maintain in the blood for the use of the body the iodine content of the sea, and may thus have made possible the evolution of the land animal" (Rogers, 1927). The temperature of a poikilothermic animal in any environment is as a rule a little higher than that of its surroundings. Such animals may raise their body temperatures a little by increasing their metabolism. Smith (1930) estimates that 15% of the metabolism of an active Protopterus is expended in muscular movements. On the whole, poikilothermic animals are at a disadvantage because many of their activities must be suspended when temperatures fall. When they leave aquatic habitats, where the high specific heat of water makes rapid change in temperature infrequent, they are often confined to situations where the environment prevents rapid changes. The soil, leafy ground litter, rotting logs, and similar refuges are

commonly sought during cold or dry periods by primitive terrestrial animals.

Homeothermism is perhaps the most important adaptation that animals have made to terrestrial life. By developing for living cells a favorable internal environment which remains quite constant chemically and thermally, animals have thus become more or less independent of environment (Pike and Scott, 1915; Pearse and Hall, 1928). The continual, rapid metabolism of homeothermic animals has the disadvantage that large quantities of food must be available. The development of nutritious land plants was associated with and to some extent conditioned the development of homeothermic land animals (Berry, 1920). A mouse at the same environmental temperature produces twenty-five times as much heat per day as a fish of the same size (Rubner, 1924). A poikilothermic animal may live for years without food, but a homeothermic animal dies of starvation in a few months.

Benedict (1932) has made an extensive study of the differences between poikilothermic and homeothermic animals. He finds that the temperature of the latter is higher than that of the former at any environmental temperature. A poikilothermic vertebrate warmed to 37°C. produces only one-third to one-eighth as much heat as a homeothermic vertebrate. Benedict, after examining various possibilities, concludes that differences between the two are not due to differences in protoplasm, chemical constitution, or metabolism, though poikilothermic animals do contain more water and ash, less dry matter and active protoplasmic tissue than homeothermic animals. The heart rate is higher and there is more blood in homeothermic animals. "It is therefore believed that the *distribution of the blood* in the tissues may explain the difference in the metabolism of these animals. . . . Where there is a liberal supply of blood to the tissues

heat production *can* be high. Where the blood supply is low, it *must* be low. . . . All these considerations lead to the conclusion that the distribution of the blood is the dominant factor in metabolism and that the higher metabolism of warm-blooded animals may be explained by the fact that in their case there is better distribution of blood to the outer tissues and peripheries." In mammals blood corpuscles are smaller than in fishes and amphibians. This increases relative surface and oxygen-carrying capacity.

LOCOMOTION

There is no essential difference between the locomotor organs of marine and freshwater animals, but those of animals which have left aquatic habitats to take up life on land have often been obliged to undergo considerable modification. In transferring its activities from water to land an animal enters a rarer medium and thus has an opportunity to move with a greater speed, but it cannot do this if it does not have sturdy locomotor organs which are able to support its body against the greater pull of gravity which results when the buoyancy of water is lost. Seals and whales are powerful and agile swimmers, but on land are awkward or incapable of locomotion.

The chief invaders of the land are: (1) animals which creep on slimy muscular surfaces, such as flatworms and snails; (2) those with hard exoskeletons, the arthropods; (3) and those with endoskeletons, the vertebrates. Terrestrial worms and molluscs have remained subterranean or are confined largely to moist situations. None has attained speed, which Jehu (1923) maintains is a primary quality of a typically terrestrial animal. It is the arthropods and tetrapod vertebrates which are today the dominant land animals.

Arthropods in any habitat are covered with a chitinous exoskeleton, which is also often impregnated with mineral salts and

thus strengthened. Their jointed legs are suited for locomotion of various types. They may be flattened and provided with long bristles, thus serving as admirable organs for swimming, or they may be provided with stout spines which hold fast when an animal runs on land. Arthropods appear to be related to annelids. In fact, if some polychaete annelids were to be provided with an exoskeleton, they would become annelids without further modification. Harms (1929) has described a tough-skinned polychaete which walks about on land by using its parapodia somewhat as a centipede uses its legs. Land crustaceans have stouter, more spiny and less setose limbs than their aquatic relatives; but a strictly aquatic crab which is suddenly placed on land is not unsuited to locomotion and, if permitted, quickly makes its way back to water. The locomotor difficulties of arthropods in attaining land life have been few and simple.

The origin of the tetrapod limbs of vertebrates is more or less of a mystery, but palaeontologists and comparative anatomists rather generally agree that they came from lobe-fins such as crossopterygian ganoids possessed in Devonian times. "The tendency toward the evolution of freely turning paddles, presumably out of fin-folds, reaches a climax among the lobe-finned fishes of late Paleozoic times . . . the paddles spread out like the sticks of a fan, and the bony rods that support them seem destined to give rise to the skeleton of the arm and hand in higher vertebrates" (Gregory, 1933). "At all events it is clear that we should expect the fish-like ancestors of the Tetropoda to have possessed pectoral and pelvic fins alike in structure, with outstanding muscular lobe, extensive endoskeleton with at least five radials, small web, and few if any dermal rays" (Goodrich, 1930). Lull (1929) believes that the earliest tetrapod limbs may have been two-toed but agrees with others that the majority of primitive land vertebrates were five-toed.

The limbs of certain modern fishes which live out of water on muddy beaches have been described in considerable detail (Hamburger, 1904; Eggert, 1929a). The ventral, or posterior, fins of gobies often together form sucker-like organs which are used for locomotion on land and even for climbing. In land gobies there is a tendency to have a broad cleithrum at the base of the fin; the basal bones often fuse; fin rays are short and few; and special muscles develop for walking which are not present or poorly developed in aquatic gobies. Changes from aquatic to land life involve better muscular development and nervous coördination (Pike, 1924).

NERVOUS SYSTEM

As animals have progressed from aquatic to land life, they have attained greater speed in their locomotor responses to stimuli, and more dependence has been placed on sense organs which give distance, rather than contact, perception, and more effective mechanisms have been developed for the control of bodily activities. Hormones, which in primitive metazoans are probably produced more or less by cells throughout the body of an animal, come to be secreted by definitely localized organs and are integrated with nervous mechanisms for the control of bodily functions.

In the ocean, where small organisms suitable for food float everywhere in the water and accumulate as oozes on the bottom, radial symmetry, with its decentralizing influences on nervous organization, is common. But on land there are no radially symmetrical animals. Terrestrial, bilateral types show progressive cephalization and delegation of bodily control to nervous mechanisms, which perhaps have reached their climax in arboreal and aerial animals.

The eyes of terrestrial arthropods are often very large com-

pared to those of types that live in water (Harms, 1929) and come to constitute a considerable portion of the nervous system (Kennedy, 1927a). The ghost crab, Ocypode, can see objects clearly at distances of 10 to 15 meters (Harms, 1929). The compound eye of an agile insect predator, such as a dragon-fly or a robber-fly, are very acute and may be made up of thousands of simple eyes. Stridulating organs are rare among aquatic arthropods, but the songs of land types are well known. Organs of hearing are proportionally well developed. Sensory hairs and gustatory and olfactory organs change their character completely when arthropods change their habitat from water to land (Marcus, 1911; Harms, 1929). Odors are important in the daily life of many land crustaceans (Borradaile, 1903; Harms, 1929) and constitute the basis for the social life of insects (Kennedy, 1927a). Some polychaete worms which live on land have sense organs which resemble those of arthropods (Harms, 1929).

The eyes of fishes which live on land have been much studied (Beer, 1894; Baumeister, 1913; Hess, 1913; Harms, 1914, 1929; Weve, 1922; Karsten, 1923; Schreitmuller and Relinghaus, 1926). The climbing perch (Anabas) has eyes like aquatic fishes, and is myopic in water and on land. The beach-skipping gobies belonging to the genus Periophthalmus, however, differ from other fishes in being hypermetropic and in other respects are adapted for life on land. In common with other fishes which live in mud these gobies have a liquid-filled chamber in front of the cornea for protection. They are unlike other fishes in having to accommodate their eyes for near vision, in having the eyes protruberant and quite movable, and in possessing a considerable degree of binocular vision. A beach-skipper can see a termite clearly at a distance of two to three meters.

Amphibia furnish favorable material for the study of changes in sense organs with the assumption of terrestrial life, because

many of them spend part of their life on land and part in water. Matthes (1927) has investigated the olfactory organs of the European newt (Triturus). He finds that when a newt is changed from water to land there is a temporary loss of ability to smell, but recovery takes place after three or four days. The nasal epithelia are quite different in land and water newts. The olfactory hairs in the former are five times as long as those in the latter. If a terrestrial newt is replaced in water, its olfactory hairs soon shorten.

EXCRETION

"All organisms which have the power of regulating the osmotic pressure of their body fluids are provided with an excretory organ corresponding to a kidney" (Wardlaw, 1931). Probably the primitive function of renal organs was to regulate the osmotic pressure of internal fluids, and only secondarily have they assumed the elimination of metabolic wastes. All animals which live in freshwater, where the external medium is hypotonic to their body fluids, readily permit the return of water from their bodies to the outside. A Paramecium in 24 hours may eliminate water equal to 31 to 700 times its own volume, depending on temperature (Hesse, 1920).

The water-eliminating activities of kidneys are as a rule greater in freshwater than in the sea or on land because animals there live in solutions that are hypotonic to their body fluids. Crabs usually do not eliminate water through their kidneys, but crayfishes, freshwater fishes, and amphibians do. Most marine crustaceans have urine which is isotonic with sea water, but freshwater amphipods have larger kidneys than those that live in the ocean and excrete more water through them (Schlieper, 1933). The green gland of the land hermit crab, Coenobita, is reduced and lacks a terminal vesicle, thus differing from

comparable marine crustaceans (Borradaile, 1903). "The glomerular development of the kidneys of vertebrates is related to water excretion. The protovertebrate kidney was at one stage probably aglomerular, and the glomerulus was evolved as an adaptation to a freshwater habitat. In the lower vertebrates remaining in freshwater (dipnoans, ganoids, and freshwater teleosts), and those still in intimate dependence on it (Amphibia) the glomerular development is good; but with the secondary assumption of marine habitat (marine teleosts) or with the assumption of terrestrial life in which water-conservation becomes a necessity (arid-living reptiles and birds) the glomerular development is poor" (Marshall and Smith, 1930). Mammals have modified the glomerulus into a filtration-reabsorption apparatus. Cyclostomes and elasmobranchs are like freshwater fishes in glomerular development. Fishes transferred from sea water which is hypotonic to their body fluids to that which is hypertonic may, if they live, excrete salts through their kidneys (Schlieper, 1933; Smith, 1933). Frogs in water at 20°C. excrete water at the rate of 1.3% of their body weight per hour (Adolph, 1927a). Their urine is always hypotonic to their body fluids. But if the skin is dried or if the body is in hypertonic solutions a frog may absorb water from the bladder into the tissues (Steen, 1929). A man excretes a fiftieth of his body weight per day through his kidneys; a frog at ordinary temperatures, about a third.

Kidneys in all animals may more or less perform two functions: (1) the regulation of the concentration of body fluids by conserving or eliminating water and solutes and (2) the excretion of the waste products of metabolism. Elasmobranchs retain urea in their blood to increase osmotic pressure (Scott, 1916; Dennis, 1922); estivating lung-fishes may retain large quantities of urea in their bodies because water for its elimination is not

available (Smith, 1931). Many birds and desert reptiles excrete uric acid instead of urea, and thus conserve water, for the former is practically insoluble. The evolution of the forms that nitrogenous wastes take in various invertebrates (Delaunay, 1929) and vertebrates (Perzylecki, 1926) is interesting, but not particularly significant in connection with aboceanic migrations except for the fact that changes have had relation to environmental conditions.

REPRODUCTION

The eggs of some animals require salt in the surrounding medium for their development. "This dependence of the egg on the inorganic material of its evironment . . . seems to be a significant limiting factor, making it impossible for marine animals to colonize freshwater, until, by some chance mutation, perhaps, the capacity for providing enough ash within the egg is acquired. To the factors defined by Sollas and von Martens we must add the importance of the freshwater egg being supplied with materials that its inorganic surroundings cannot be expected to give it" (Needham, 1930). "The ova of Nereis are capable of fertilization and development in thirty-three and one-third per cent sea water" (Just, 1930, 1930a), but those of Echinarachnius and other marine animals die in rather slight dilutions. An eel, after a prolonged sojourn in freshwater, is prepared to reënter the ocean and lay its eggs by the increase of osmotic pressure in its body fluids, and this apparently occurs without any stimulating change in its surroundings (Johnstone, 1908). Gastrotricha show an interesting reaction to salinity. In the ocean they produce an abundance of males and zygotes, but in freshwater reproduction is parthenogenic (Remare, 1929).

As some animals are limited to life in the ocean by salinity requirements, so some are kept in aquatic habitats by inability to carry on reproductive activities in the absence of water. The

eggs of most fishes and amphibians are laid in water, but a few deposit them in air so that hatching young fall into the water. The spotted salamander, *Ambystoma maculatum* (Shaw), lays its eggs in ponds, but spends most of its adult life on land. Blanchard (1930) has studied the breeding habits of this species. "Migration to the breeding ponds depends on rain and not on temperature . . . in southern Michigan the spotted salamanders begin migration to the breeding ponds during the first rain at night following the disappearance of snow and thawing of the surface of the ground in the woods; . . . a prolonged rain, or several rains, will be required to bring all adult individuals of the species to the breeding sites." The marbled salamander, *Ambystoma opacum* (Gravenhorst), drowns in water. Its eggs are enclosed in four capsules and hence are fitted to some degree for life on land. They are usually deposited in situations where hatching tadpoles will be washed into water by rains; but will hatch on land as well as in water (Noble and Brady, 1933). They will not hatch without considerable moisture, and tadpoles usually emerge during rains. Salamanders of the genus Plethodon have left the water during all stages in their life cycle. Their eggs are to be found in moist situations under logs and stones or in holes in the ground. The tadpole stage is passed within the egg membranes before hatching.

The chief reproductive adaptations which have enabled animals to leave the ocean and take up life in freshwater and on land are as follows: (1) Internal fertilization, which permits the union of gametes without reference to the character of the external medium. The union of gametes of many species takes place readily in freshwater but is of course impossible in air. Many male animals in marine, freshwater, and land habitats produce spermatophores which are left to be picked up by, or actually injected into, females of the same species. (2) A shell,

which protects and insulates—conserves water and salts; protects from desiccation and injury. (3) Food provision—as yolk in the egg cell, within the body of a parent through such structures as placentae, or even by the feeding of young, as by bees and birds. (4) Reduction in the number of young and better care of them by such membranes as those about eggs and the amnia of insects, birds, and mammals; by watchfulness and care by parents of eggs or young. Care may extend even to the keeping of the young warm by placing them in favorable situations or by heat from the parent's body and to education for the work of adult life. (5) Reduction of free-swimming larval stages and a general tendency toward viviparousness. (6) Adoption of peculiar breeding habits to avoid interspecific competition. The grunion deposits eggs in sand above the water, and other smelts leave their eggs in the sea. The species of shrimps in Chesapeake Bay breed at different seasons (Cowles, 1928). "The terrestrial stage in the life of *Ambystoma opacum* is an adaptation permitting the species to compete successfully in the same region with other species of *Ambystoma*" (Noble and Brady, 1933). Of course no single quality of those enumerated is absolutely characteristic of land or freshwater, but they indicate trends. There are marine elasmobranchs which nourish their young with secretions from the mother's uterus (Alcock, 1902).

In life cycles animals may show nicely graded series of stages connecting specialized with primitive conditions or individuals, races, or species may be sharply segregated from others. Land crustaceans, which came originally from the sea, either produce marine free-swimming larvae from their eggs (Coenobita, Birgus, Uca, Cardisoma, Gecarcinus) or they do not (crayfishes; river crabs, Potamon). There are no intergrades. The littoral isopod, *Ligia baudiniana* (Milne-Edwards), commonly avoids sea water and, when wetting its gills, carefully keeps its

body from contact with it, but does not free its young from its brood-pouch unless submerged. The British littoral snails of the genus Littorina furnish a nice series of variations in breeding habits: *L. litorea* (L.), lowest on the beach, produces eggs which hatch out early veliger larvae; *L. obtusata* (L.) in the mid-tidal zone lays eggs which hatch out second stage-veligers; *L. saxtilis* (Olivi) and *L. neritoides* L. are viviparous, and thus best adapted to the dryer conditions near high-tide mark (Colgan, 1910; Flattely and Walton, 1922).

Some animals in their life cycles reproduce events which represent critical transformations that their ancestors struggled to attain in the past. A tadpole when it metamorphoses into a frog changes and improves its powers of regulating osmotic pressures within its body, and the acquirement of this new ability is simultaneous with the cessation of the use of the gills (Adolph, 1927b). A few fishes "undergo a certain metamorphosis into partly terrestrial animals, and Harms found that this metamorphosis was influenced by the thyroid hormone, as in the case of Amphibia" (Noble, 1931). The land hermit crab, *Birgus latro* Leach, when young inserts its twisted abdomen in a snail's shell, like other hermit crabs. As it grows larger, it finally is unable to find a shell big enough for its abdomen, which then becomes bilaterally symmetrical and bears hard chitonous plates on its dorsum (Harms, 1932).

The development of an animal requires a certain environment, which in many cases is the sea or is a sea-like liquid enclosed within an egg shell. Energy is also necessary, and, as a rule, much of this is supplied from food stored in the egg itself, but at times it is supplied from other sources, such as secretions from a parent or other foods. A variable environment, if it is not too dry or too cold, tends to hasten development (Shelford, 1929). Land habitats, because they vary more, in general are

populated by animals which show well-marked seasonal rhythms and often have very brief developmental periods unless the young are retained within the body of the parent or live in some special terrestrial habitat where conditions of life are constant. For example, the tadpoles of highly terrestrial amphibians have shorter lives than those which are more aquatic. A spade-foot toad tadpole transforms into an adult in two to four weeks after hatching, but a bullfrog tadpole lives for a year or two (Wright, 1931).

Reproductive and growth processes are more or less rhythmic and are usually orderly and cyclic (Flatterly, 1920; Brody, 1928; Adolph, 1931a). In stable, uniform environments, such as the open ocean furnishes, animals are often erratic and perennial, but in the littoral marine region, in freshwater, and on land they are usually definitely correlated with seasonal successions. Hubbs (1928) believes that in fishes "structural differences between local races seem largely the result of changes in developmental rate (and metabolism), not themselves of direct selectional significance. A harmonious relation exists between the developmental rate and the usual environmental conditions during growth. Normal development is possible with some variation in conditions. But when a new territory is populated, with, for instance, a lower temperature, the individuals are brought closer to the threshold of abnormal development, and a higher rate of elimination must result. A mutation covering the developmental metabolism would adjust the population to the new habitat. Such changes as an increase in segments would secondarily result. The population would increase and push on into still colder waters, where the same modifications would be expected. A series of such primary physiological and secondarily structural alterations would produce the graded series of local races often exhibited in the latudinal variation of fishes."

FOOD

As has been pointed out (p. 78), animals that live in water are surrounded by food in the form of small plants and animals and as dissolved substances. In the ocean algae of some size and a few higher plants are present alongshore, but these constitute a very small part of available food resources. In freshwater a considerable body of submerged and emergent vascular vegetation is available. On land the bulk of the plant food of animals is made up of spermatophytes. Pütter's (1909) idea that aquatic animals absorb considerable amounts of organic food through external bodily membranes seems to have been pretty well disproved (Dakin, 1925), but some aquatic animals undoubtedly do utilize such nourishment as colloidal material which is taken from water passed through the enteron (Hinmon, 1932; Smith, 1933).

In any habitat animals tend to be specialists in their food relations, although there are always omnivorous animals of both specialized and generalized types. Animals commonly avoid competition by using different foods (Pearse, 1930, 1934). Along the shores of aquatic habitats the majority of animals are vegetarians, mud eaters, and scavengers (Pearse, 1929, 1932a). Carnivores must always occur in smaller numbers than the animals upon which they prey. Animals which have attained terrestrial life have been obliged to restrict their digestive activities to the interior of their bodies. Organs of taste, instead of being scattered over the outside surfaces, are limited to the region about the mouth (insects) or to the buccal cavity itself (land vertebrates). In finding foods more dependence is usually placed on organs (olfactory, visual, auditory) which receive stimuli from a distance. Glands along the digestive canal are more sharply defined. Water is added to food by salivary glands near the anterior end of the alimentary canal and re-

moved from it near the posterior end. A snail's radula, which is an old organ developed in the ocean, is an admirable mechanism for rasping off bits of land plants for foods. A carp has no stomach and no peptic digestion (Kenyon, 1925); there is much enteric variation among fishes according to food habits. Among mammals there are many differences in food habits, but there is comparatively slight variation in organs of digestion. There is no mammal without a stomach. A primary distinction between reptiles, as terrestrial types, and amphibians, as aquatic types, is in the teeth, which in the former are more firmly fastened into the jaws. Mammals make further improvements in teeth. They usually have two successive sets and have enamel-covered surfaces which effectively grind up hard terrestrial plants. Birds in modern times all have horny beaks which tear flesh, strain small organisms from water, or crack hard seeds of vacular plants. Their gizzards grind up resistant foods.

The animals which have taken advantage of the food resources on land, though consuming a great variety of foods, are on the whole representatives of a few specialized groups which by particular adaptations have taken advantage of the great stores of organic foods in land vegetation.

ACCLIMATIZATION

Animals which change from one habitat to another must acquire new ranges of toleration for environmental factors. The degree of acclimatization that an animal undergoes may be judged by changes in its ability to survive extreme conditions, by its success in populating new habitats, or its behavior after being subjected to changed conditions (Shelford, 1929). The mechanisms for acclimatization appear to be concerned with modifications in the character of protoplasms. At times they may be shown to consist of loss of water, changes in metabolic rate, or

other measurable variations, but the factors concerned in many of them are still unknown.

Animals which have entered brackish water from either sea- or fresh-water may be small in size (Schlieper, 1933). In some of these oxygen consumption may decrease as much as 25%. The activity of surface membranes and excretory organs may be inhibited. Other animals that readily adjust themselves to changed salinities usually use more oxygen in diluted sea water for a time, and may become more or less "febrile." A marine animal migrating from the ocean into fresher water needs more energy and, if it cannot supply it, is inhibited in various ways. Andrews (1925) tested the resistance of sixteen species of littoral animals to variations in temperature, acidity, salinity, stagnation, and light. He found that young animals usually died more quickly than old when there were extreme variations, but that the former had greater capacity for acclimatization if changes were gradual. Young animals probably died quickly on account of their surface-mass relations and more rapid metabolism. Old animals were less resistant to acidity, probably on account of a more limited alkali reserve.

Growth is probably an autocatylitic process (Robertson, 1923). Its rate changes abruptly at certain critical temperatures (Crozier, 1929) and in response to other environmental changes. Hence variations in an animal's environment may cause changes in metabolism, lack of growth, or death. Rate of growth and metabolic activity commonly change with age (Burge, 1921). Variations in temperature alter equilibrium constants of chemical reactions and the relative proportions of reacting materials. It is therefore usually easier for an animal to adjust its activities to a lower than to a higher temperature (Wardlaw, 1931). As would be expected, aquatic animals vary greatly in their ability to resist the extreme variations in temperature, salinity, and other

factors which accompany landward migrations. Starfish larvae have little ability to adjust themselves to higher temperatures, but ciliates have (Jacobs, 1919). A fish consumes three times as much food at 20°C. as at 10°C. (Hathaway, 1927). Animals can, if subjected to altered environmental conditions, alter their range of activities to some extent, i.e., they become acclimatized to new levels (Davenport, 1908; Huntsman, 1924a, 1924b; Gompel and Legendre, 1927). As time for its metamorphosis approaches, a toad tadpole loses much of its ability to endure high temperatures (Hathaway, 1928). As it prepares for land life, it acquires new powers and loses old abilities. Adjustments usually involve such compensations in the way of acquisitions and losses.

Acclimatizations often result in rhythmical adjustments to regularly recurring variations in environment. As such variations are more extreme in land and freshwater habitats than in the sea, animals in the former generally show more striking adjustments than those in the latter. The differences between the habits of nocturnal and diurnal animals, for example, are on the whole greater among land animals than among those in the ocean. When the environment is most variable, ranges of physiological endurance and adjustment are usually wider. Under such circumstances it is not strange that homeothermic animals, while enjoying the stimulating uncertainty of life on land, have attained some degree of stability by having constancy in internal fluids which bathe living cells and in body temperatures.

Kennedy (1925) has "come across two species of insects, one a dragonfly, the other a mayfly, in which a reversal of one or more of the tropisms normal to the other species of the same genus has permitted the entrance of these reversal species into environments not open to normal members of the genus." These

insects have made adjustments which have given them special advantages by forsaking traditional modes of behavior for their types.

Acclimatizations may be concerned with resistance, toleration, enlarged or restricted ranges of adjustment, changing tropisms and habits, or other things. They usually involve complex groups of activities, but the net results permit animals to live in a changed environment.

PARASITES

In the ocean many animals are associated with others as commensals, symbionts, or parasites, but such relations are not usually carried over into freshwater and land habits. Parasites show a general tendency to become specialists in their host relations. Many are restricted to a single species, genus, or family, though there are also numerous wide-ranging types. Parasites are often used as indicators of the past history and relationships of their hosts (Metcalf, 1929).

Parasites that occur in and out of the water alongshore are of special interest in connection with aboceanic migrations. In such widely separated localities as the coasts of China, Japan, and Dry Tortugas (Pearse, 1929, 1930a, 1931) the land crabs alongshore carry more parasites than crabs in the ocean. Some of the terrestrial parasites (mites) evidently were acquired on land, but even such types as certain species of parasitic copepods (Wilson, 1913; Pearse, 1930b) and commensal vorticellids (Pearse, 1930a, 1932c) are seldom found on aquatic crustaceans and are quite common on similar terrestrial hosts. Probably some parasites are more common on terrestrial types because the bloods of such hosts are more stable and nutritious than those of their more primitive relatives in the ocean, but the consistent presence of others is not so easy to explain. In Japan a rather careful

survey of the parasites of eight species of salamanders which ranged from aquatic to terrestrial types showed some peculiar anomalies which were apparently due more to host specificities than to habitat relations (Pearse, 1932f). Among protozoans: Trypanosoma and Balantidium were found only in an aquatic newt; Trichodina only in the bladder of a land salamander that bred in water; and Opalina and Endamoeba in a land salamander. Amphistomes, distomes, and Rhabdias were found only in aquatic salamanders; Gorgoderina and cestode cysts were found only in terrestrial salamanders. At the mouth of the Menam Chao Phya in Siam the aquatic crabs had more parasites than those on land, largely because two species of large porotunids often had their gill-cavities filled with barnacles (Pearse, 1933a); the land gobies also had fewer and different types of parasites from those that lived in the river itself (Pearse, 1932). The writer has spent several years trying to discover significant differences between the parasites of related aquatic and terrestrial animals. A few facts have been discovered, but on the whole the results are as yet disappointing, perhaps largely on account of host specificity. More work is needed.

CONCLUSION

Animals that have left the stability of the ocean for the greater environmental instability that obtains to some extent in freshwater and to a greater degree on land have been obliged to modify their internal stabilities to keep pace with external changes. Their skins have grown more selective in permitting or preventing the passage of solutes and finally have been modified to conserve body water and regulate temperature. Respiratory organs have changed so that breathing has been transferred from external water-bathed gills to internal, moist pulmonary cavities. Body fluids have changed from salty solutions closely

resembling sea water to hypertonic but less saline, nutritious, viscid, gas-transporting media which maintain standard and rather constant concentrations. Metabolism has come under the control of many regulatory mechanisms and on the whole proceeds more rapidly. Land animals generally live faster than aquatic animals, partly because they have continual access to large amounts of oxygen and partly because they live in a more changeful, and therefore a more stimulating, environment. Freshwater animals generally live faster than marine animals because they continually have to expend energy to maintain the osmotic equilibrium of their internal fluids. Locomotion has become swifter, better controlled, and more purposeful. The nervous system has acquired better correlating mechanisms and greater centralization of control. The sense organs have become better adapted for distance perception, and less dependence is placed on contact sensations in making rapid adjustments to changes in environment. Excretory organs which perhaps began as regulators of osmotic pressure have taken over the elimination of metabolic waste products, especially those containing nitrogen. Reproductive functions have been improved and adapted by internal fertilization; protection of young from thermal changes, desiccation, and other dangers; and by the nourishment, care, and education of the young. Adaptations have been developed for the utilization of the great food resources in land habitats; especially the products of hard, but concentrated and nutritious, vascular plants. Through slow acclimatization to new conditions animals have changed from sluggish systems of activities in a uniform environment where little energy is available to active, speedy systems. Land animals by keeping their internal mechanisms uniform and by moving at a rapid metabolic rate are able to live successfully in a variable environment where much energy is available.

Chapter V

WHAT LAND ANIMALS HAVE ATTAINED

ONLY one-fifth of the species of animals on the earth are aquatic (Harms, 1929). Though conditions of life on land are in some respects severe, they appear to have been, and are today, favorable for the formation of new species. Animals which have struggled up the long evolutionary trail from marine and freshwater habitats and stand today on dry land are the dominant ones of the earth. They are the successful. What is success? Has the struggle been justified?

Success is continual improvement (Pearse, 1926a). It is the result of competition for a place to live. There are of course various degrees of success. The mere fact that an animal is alive is a certification that it is to some degree successful. Among land animals, ants exceed all other types combined in individuals (Wheeler, 1910). They are successful and dominant among those which have attained land because they are progressive yet generalized. Ants are active, keen of sense, modern, and so progressive that they have built up a social organization that has long excited wonder and admiration among successful, dominant, and social vertebrates. Yet ants have not generally limited their food to one or two peculiar substances, as the honey bee has, and they have not lost the thermal and aqueous stability that goes with close association with soil. A successful animal is both plastic and progressive. It must always live in the world as it is and to some extent do such living with greater efficiency than its rivals.

Animals which struggle may look down with more or less contempt on those which are able, by lurking in the crevices or the slack waters of evolutionary currents, to find soft berths where they may exist without a struggle. Such degenerates pay the penalty exacted by the Gods of Biology. When they cease to struggle, they lose their abilities—they not only retrogress in power, but also lose appreciation. Every barnacle starts in life as a free-swimming nauplius with eyes and other sense organs. Barnacles which settle on rocks alongshore to enjoy life, where waves and tide perennially insure food and certain favorable conditions of life, lose their eyes, and thus to some degree their power to appreciate things outside themselves. Barnacles which go farther down the road which leads from struggle likewise start in life as apperceptive nauplei; but they attach themselves, not to sturdy rocks, but to other animals and lose all semblance to struggling crustaceans. As adults, they are rotund masses without legs or sense organs. They send root-like absorptive organs into their unlucky hosts and thus steal food; their bodies become soft sacs which produce myriads of eggs. They have a certain success—they continue to live, but they are degraded, specialized, and limited. Land animals because they live in a changeful environment are stimulated to be alert strugglers.

If it is desirable to move speedily and handle problems encountered in environment with increasing understanding and efficiency, to be progressive, then the struggle to land has been worth while. Speed is a primary quality of land animals (Jehu, 1923). They live in a rarer medium than aquatic animals, and in the atmosphere an abundance of oxygen for metabolic activity permits them to live faster (Krogh, 1916). Fast living requires a continual supply of nutritious food, which is available in land plants, and for terrestrial animals this is

supplemented by a greater quantity of radiant energy than is to be had in aquatic habitats. Kennedy (1928) has pointed out that insects are generally distributed in relation to available energy according to their degree of specialization. The primitive insects frequent moist places close to the soil and are often nocturnal; specialized insects fly in the open sunlight when time of day and season of year make most energy available.

One quality of terrestrial environment is variability. This has been a factor in the development of that most effective adaptation to land life—homeothermism. Birds and mammals, which keep their body temperatures and their body fluids close to optimum conditions for cell activity, are so independent of environment that they can, if stored energy is available in the form of food, live in polar regions and tropical deserts where life is impossible for poikilothermic land animals. Homeothermism makes continuity of activity and thoughtful endeavor possible.

The variability of land habitats stimulates animals to greater activity and versatility in response to environmental changes. It is on land that animals have developed greatest ability to solve complex problems. The most astute thinkers are land animals. Even on land monotony is conducive to lack of progressive accomplishment. Man has not done his greatest works in the tropics, where much radiant energy is available and temperatures are always high; conditions of life are too monotonous. The most progressive modern races and nations are found in temperate regions where humidities and temperatures vary. In such localities men are most healthy, competent, and productive (Huntington, 1927).

Perhaps the fairest flower of progressive evolutionary growth on land is human civilization. This is the product of homeothermism, which permits continuity of activity, social life,

which multiplies and strengthens individual accomplishment and, by the overlapping of generations and the accumulation of works in the way of social procedures, homes, inventions, libraries, etc., also contributes to continuity of cumulative activity. Man through knowledge has means for controlling environment or compensating for changes in it. Such extra-corporal assets are far above those at the command of any other animal. He is able more or less to keep conditions outside his body stable. Civilized life thus tends to become monotonous, and man suffers ennui. He yearns for excitement. A savage is continually busy escaping dangers and finding enough to eat. A civilized man has leisure, which is a luxury that only a few animals enjoy. How man shall spend his leisure time is perhaps the chief problem of organized human society today. Joad (1928) compares man to a child with a box of matches—science has given him leisure, and he does not have wisdom enough to know what to do with it. The reason is that knowledge and opportunity have not changed the primitive nature of man (Schiller, 1924). The quick and astute continue to exploit the slow and unprogressive. Abilities differ and all cannot be reduced to a common level. If one man elects in his spare hours to improve his abilities by study or practice, society should reward him. Another man who chooses to sit in idleness or waste himself by keeping busy with the trivialities of life should be penalized. Organized work is a product of society. It is today the best tool which may contribute to the attainment of success. But it must not be just work, such as satisfies industrious natures; it must be thoughtful and purposeful work.

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